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ECOLOGY

ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

OFFICIAL PUBLICATION OF THE
ECOLOGICAL SOCIETY OF AMERICA
CONTINUING THE PLANT WORLD

46439
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VOLUME 24, 1943

46439

PUBLISHED QUARTERLY
IN COOPERATION WITH THE ECOLOGICAL SOCIETY OF AMERICA
AT PRINCE AND LEMON STREETS, LANCASTER, PA.
BY THE
BROOKLYN BOTANIC GARDEN
BROOKLYN, N. Y.

ECOLOGY

A QUARTERLY JOURNAL
DEVOTED TO ALL PHASES OF ECOLOGICAL BIOLOGY
Established 1920

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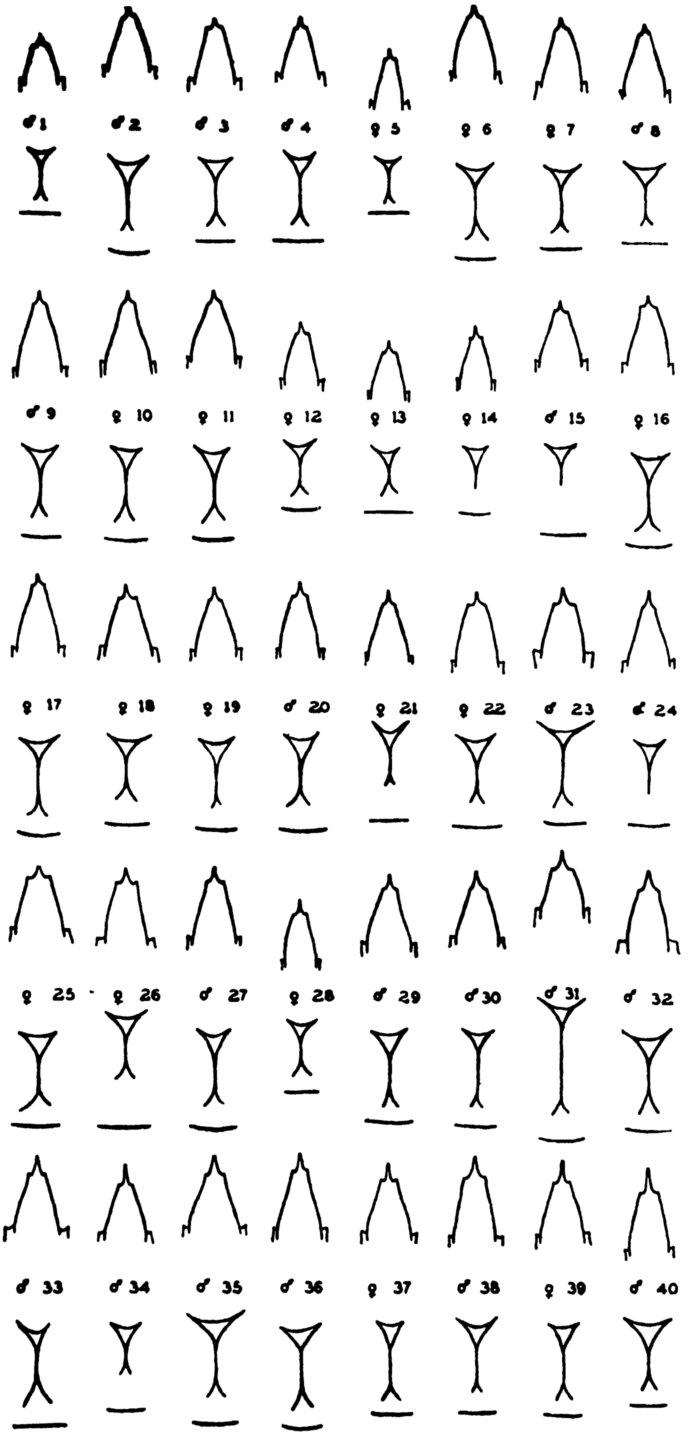

FIG. 2. Outline drawings of forty *C. clarkii* selected at random from one collection to illustrate the variation of the rostrum, areola and carapace proportions.

later an analysis of 155 *C. clarkii* of all sizes was made. The figures showed definitely that the correlation between the length of the cephalothorax and the length of the abdomen averages 1.00, with little variation.

Aside from variations such as deformed appendages due to injuries, there also was noted variation in the shape of the carapace, areola and rostrum, especially the latter. It was possible in a sample of 40 adult *clarkii* selected at random from one collection to find every shape of rostrum from one without spines to those with very prominent spines, and also great divergences in relative proportions of the parts of the carapaces.

The drawings (figure 2) delineate these variations more strikingly than description, and the whole may well serve to further emphasize the difficulties of placing too much confidence in species descriptions based on only one or a few individuals. The figures have been placed as much as possible in a graded series based on the spinosity of the rostrum, beginning with an almost spineless form (no. 1) and passing gradually to those with lance-like tips and prominent spines (nos. 38, 39, 40).

PREVIOUS WORK ON THE LIFE CYCLE OF *C. clarkii*

In a survey of the literature of the species only three or four references are pertinent to an understanding of the developmental cycles. Faxon ('85) noted certain peculiarities of the young stages of *clarkii,* and Andrews ('06) noted a few data of its life history. Again, in 1907, Andrews presented excellent notes and drawings of the development of the attached young of *clarkii.*

Viosca ('31) also recorded a few data of the life history of *clarkii.* He found them eating aquatic plants, especially *Sagittaria* spp., *Alternanthera* sp., *Polygonum* sp. and *Jussiae* sp.

Martin and Uhler ('39) reported that *C. clarkii* feeds on *Chara* sp., *Anacharis* sp., *Naias* spp., *Potamogeton* spp., blanket algae and some other aquatic plants. *Myriophyllum* sp. and *Marsilea* sp. were reported as not eaten.

More recently, Viosca ('39) in an article of popular nature gave additional information on the life history of *clarkii.*

A study of several aspects of the life history of *clarkii* was begun by the present writer in the fall of 1938 and was actively pursued through February 1941. The study reported here tried to stress particularly the changes of populations of the species due to growth, spawning, habitat changes and other factors by frequent collections and statistical analyses.[4]

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Habitat.—*Cambarus clarkii* is most abundant as a marsh inhabitant ranging from purely fresh to brackish water. In the early part of its life it is found in deeper water (up to two or three feet) in the shallow marsh lagoons. As it attains maturity and the spawning season approaches, it migrates to the shallower water of open marshes (usually less than six inches deep). At Chalmette, La., the population almost completely shifts twice annually between the lagoons and the open, slightly brackish marsh.

In the fresh-water swamps at the same time of the year the shallower ditches are

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[4] It is a pleasure to express my appreciation to Dr. F. H. Wilson, Tulane University, for encouraging the investigations which led to the completion of the study, for enthusiastic help during the course of the work, and for assistance in the preparation of this paper. Thanks are due also to Messrs. Milton L. Lindner and W. W. Anderson, of the New Orleans office of the U. S. Bureau of Fisheries, for cooperation in the tagging activities, and to Percy Viosca, Jr., who generously loaned fenced ponds on the farms of the Southern Biological Supply Co. for the tagged crawfishes in addition to advice and encouragement; to my colleagues Ruffin T. Perkins, Jr., William D. Gude, Jr., and Ernest C. Martin, for their willing assistance in making the collections; and, to Miss Mimi Harry who did the drawings illustrating variation, and to my sister, Miss Georgia E. Penn, for generous assistance throughout the course of the study.

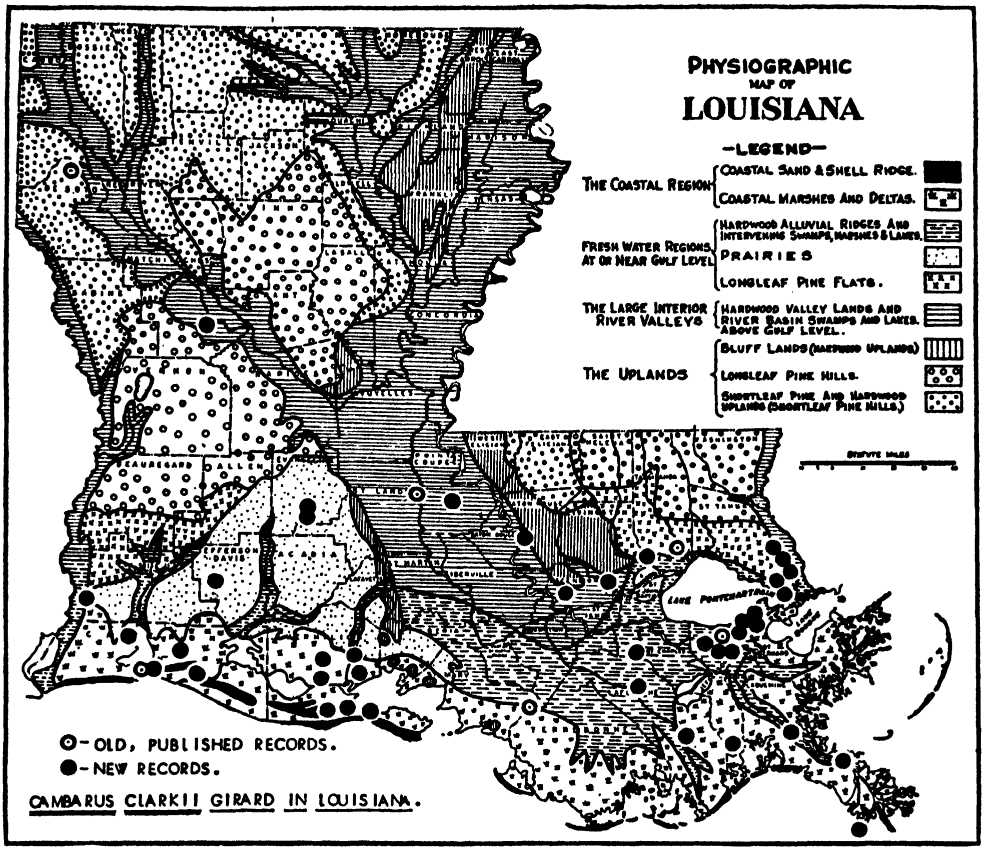
PHYSIOGRAPHIC MAP OF LOUISIANA
—LEGEND—
THE COASTAL REGION
COASTAL SAND & SHELL RIDGE.
COASTAL MARSHES AND DELTAS.
FRESH WATER REGIONS AT OR NEAR GULF LEVEL
HARDWOOD ALLUVIAL RIDGES AND INTERVENING SWAMPS, MARSHES & LAKES.
PRAIRIES
LONGLEAF PINE FLATS.
THE LARGE INTERIOR RIVER VALLEYS
HARDWOOD VALLEY LANDS AND RIVER BASIN SWAMPS AND LAKES. ABOVE GULF LEVEL.
THE UPLANDS
BLUFF LANDS (HARDWOOD UPLANDS)
LONGLEAF PINE HILLS.
SHORTLEAF PINE AND HARDWOOD UPLANDS (SHORTLEAF PINE HILLS.)
STATUTE MILES
LAKE PONTCHARTRAIN
O - OLD, PUBLISHED RECORDS.
● - NEW RECORDS.
CAMBARUS CLARKII GIRARD IN LOUISIANA.

FIG. 1. Physiographic map of Louisiana showing the distribution of old and new collections of *Cambarus clarkii.*

Louisiana are plotted on the accompanying map (figure 1). The scarcity of records of the species in the northern half of the state is explained not only by the lack of a large number of collections in that area, but probably also by the lack of habitats suitable for its presence.

C. clarkii is found in a diverse number of situations. Swamps, marshes, lagoons, bayous, and sluggish streams almost everywhere in Louisiana except in the piney-woods support varying numbers of the species. It extends even down to the coastal marshes, if they are not more than slightly brackish.

The first Louisiana record of the species was published by Hagen ('70) who recorded it from New Orleans. The other published records from Louisiana follow, arranged by parishes:

CAMERON: Cameron (Ortmann, '05);
DE SOTO: Frierson (Faxon, '14);
ORLEANS: New Orleans (Hagen, '70, Faxon, '85, Andrews, '06, '07, Ellis, '19);
ST. LANDRY: Melville (Faxon, '14);
ST. MARY: Morgan City (Faxon, '14, Ellis, '19);
TANGIPAHOA: Tangipahoa River (Faxon, '85).

MORPHOLOGICAL CONSIDERATIONS

The length of the cephalothorax was found to represent approximately one-half of the total length of *C. propinquus* by Creaser ('33) and Van Deventer ('37) in work on life cycles; accordingly the same measurement was taken as the standard when this work was begun, and,

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A STUDY OF THE LIFE HISTORY OF THE LOUISIANA RED-CRAWFISH, *CAMBARUS CLARKII* GIRARD[1]

GEORGE H. PENN, JR.

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Since Louisiana includes approximately one and three-quarter million acres of fresh-water marsh and about two and one-half million acres of salt marsh (Viosca, '28) much of which is suitable for crawfishes,[2] it is not surprising that the people of Louisiana many generations ago familiarized themselves with the edibility of the local crawfishes and have used them as an item of food for many years. The first recorded commercial catch of crawfishes in the United States was in 1880 to the extent of 23,400 pounds, valued at about $2,140.00, with New Orleans accounting for over a third of this.

The large, red crawfish, *Cambarus clarkii* Girard, comprises the bulk of the commercial crop in Louisiana, although the white river-crawfish, *Cambarus blandingi acutus* Girard, accounts for a considerable part. The annual catch for table use only was estimated by Dauenhauer ('40) at 2,193,385 pounds with a cash value of $175,470.80 for the 1938 season, which represents approximately the annual catch for the last three or four years.

DISTRIBUTION OF THE SPECIES

The type specimens of *C. clarkii* described by Charles Girard ('52) were collected between San Antonio, Texas and El Paso del Norte by John H. Clark of the U. S. Mexican Boundary Commission, for whom the species is named. Since then it has been seen only on the Gulf Coastal plain extending from eastern Alabama to western Texas and up the Mississippi valley as far north as Pulaski County, Arkansas.[3]

In Louisiana *Cambarus clarkii* has been found to be one of the most common of all the species in the state. The localities from which *clarkii* has been recorded in

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[1] A contribution from the Department of Zoology, the Tulane University of Louisiana, New Orleans.

[2] The name *crawfish* is used in this paper because it is believed to be the most common common-name for the species of crawfishes of the genus *Cambarus* to which they belong; and, it is the only common name for these animals throughout the South and in other rural sections of the United States, notwithstanding the belief of many who propound that our "crawfish" are known elsewhere by the "correct name of *crayfish*." *Crawfish* has long been credited as correct in scientific writing and not only occurs almost as frequently as *crayfish* but was used as a common name by Say (1817) many years earlier than *crayfish* by Huxley (1884). The European word *crayfish* is used by teachers of zoology probably because of Huxley's classic contribution; however, *crawfish* is still the usual term applied to fresh-water crustaceans of the genus *Cambarus* in the U. S. *Crawfish, crayfish,* or as it is sometimes incorrectly called, *crab,* come from the same root, Old German *Kreb,* from which are derived on the one hand the Modern German *Krebs* and the English *crab,* and, on the other, the French *écrevisse,* and the American and English *crawfish* and *crayfish.*

[3] Faxon (1885) recorded a dried specimen from Olmstead (Cuyahogoa County), Ohio in the M.C.Z. and doubted its validity, and Turner (1926) failed to find *clarkii* in fifteen years of collecting in Ohio, which seems to indicate the definite southern distribution of the species.

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filled with mature crawfishes, and according to Viosca ('39) in the rice-growing prairie areas in the southwestern part of the state they are caught in large quantities in the inundated rice fields. Densely grown marshes and ditches are usually avoided (or are unfavorable); local crawfishermen unerringly locate their prey by the presence of such signs as shallow muddy water, uprooted aquatic plants, and the like.

To a lesser extent, *clarkii* can be found along the edges of slightly-brackish to fresh, open bodies of water, as, for example, the Audubon Park lagoon in New Orleans. This lagoon is an artificial body of water over twenty years old, about one and one-half miles long and averaging thirty feet in width. The greatest depth is less than ten feet, with steeply sloping banks. With the exception of irregular clearing of aquatic plants along the edges, the lagoon is in a natural balance, the water level probably not fluctuating over two feet the year round. Here, and in other similar locations, *clarkii* never attains great abundance, confining itself mostly to the edges of the vegetative debris, and to the shallow drainage ditches where predators are relatively less abundant.

Diurnal Movements.—Clarkii is evidently most active at night, responding positively to twilight conditions. By shining with flashlight along the water's edge at night in the spring months one can find crawfishes of all sizes actively in pursuit of food, whereas in bright sunlight crawfishes of the same ages are concealed in surface-floating vegetation or in burrows. From these positions they venture at dusk and probably remain active until dawn. On rainy, cloudy days when the water is apt to be rather dark, they are active and only the temporarily disabled individuals (such as those in ecdysis) remain in the security of the vegetation.

Spring and fall rains, especially if the water level is below the marsh floor, stir the crawfishes to activity (probably because the fresh water floods their burrows), during which many leave the marsh and walk for short distances above ground on the levees and natural elevations. Great numbers are eaten by birds and other animals at such times.

THE LIFE CYCLE

Methods, Materials and Technics.—Methods used were observational and statistical, the intention being to lay emphasis on a study of the crawfishes in their natural habitat under natural conditions.

A regular schedule of collecting trips to one locality was proposed at the outset, but was impossible to follow in practice Days of extreme cold, flooding, drought, and changes in the habitat requirements and ecology of the crawfishes themselves were the main obstacles. However, for the most part it was possible to make representative collections, seldom less than 100 crawfishes and even as many as 700, at least every four weeks, and sometimes as often as every two weeks over a period of fourteen months.

Collections were made by several methods in all lagoons, ditches, shallow ponds and marshes in the Chalmette area, St. Bernard parish and in the vicinity of Churchill Farms at Westwego, Jefferson parish, Louisiana. During the fall and winter the animals could be taken with dip-nets at the edge of the ponds. This method was especially applicable because the majority of the individuals of the catch were of small size. During the spring and up until April, it was found practical to use a ten-foot, quarter-inch-mesh seine. By its use a larger area could be covered in a shorter time, and a fairer sample of the population (which now contained larger and more widely ranging individuals) could be obtained. Seining was supplemented every time by the use of dip-nets to check for the presence of crawfishes too small to be collected by the quarter-inch-mesh. Late April and May collections were obtained by a combination of the use of baited nets

TABLE I. *Growth rate data of C. Clarkii obtained from analyses of periodic population samples*

(Collections through May 19 at Chalmette, La.; July, August and September at Westwego, La.; October and November, 1940, at Chalmette)

Date of Coll.	Total Number in Coll.	Per Cent of Each Size Group in Collection																										
		Cephalothorax Length in Millimeters																										
		5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57
1939																												
Oct. 22	157	6.0	8.0	18.0	28.5	18.0	10.0	2.0	2.0	1.0	2.5	1.0	.5			1.5				1.5								
Oct. 29	169	7.0	14.0	17.0	25.0	22.0	7.5	2.5	3.0	.5	.5						.5			.5								
Nov. 19	229	26.5	4.0	4.0	12.0	20.0	12.0	8.0	5.0	6.0	1.5	.5	.5															
Dec. 3	94	2.0	2.0	8.0	12.0	14.0	20.0	13.0	5.0	10.0	4.0	3.0	5.0															
Dec. 9	135	1.0	1.0	7.0	12.0	18.0	10.5	15.0	6.5	9.5	7.0	3.0	5.0	3.0	1.0	.5												
Dec. 15	131	1.5	13.0	10.0	13.0	10.0	12.0	8.0	12.0	8.0	2.0	2.0	4.0		3.5			1.0										
Dec. 22	200	1.0	19.0	7.0	19.0	16.0	11.5	13.5	4.0	5.5	1.0	.5	.5	1.5														
1940																												
Jan. 13	390	.5	14.0	20.0	11.0	12.5	10.0	7.0	7.5	3.0	5.0	2.0	1.0	2.0	1.0	1.5	1.0	.5					.5					
Feb. 23	740			1.0	4.0	2.0	9.0	9.0	13.0	11.0	10.0	7.0	7.0	5.0	7.0	3.0	4.0	3.0	2.0	.5	1.5	.5	.5					
Mar. 10	374				1.5	6.0	4.0	4.5	10.0	11.5	9.0	15.0	13.0	8.0	6.5	4.5	2.5	2.0	.5	.5				.5	.5			
Mar. 31	449				.2	.2	1.0	7.0	7.0	12.0	14.0	15.0	14.0	9.5	8.0	3.0	3.5	3.0	1.5	1.0	.2							
Apr. 21	315									1.0	5.0	8.0	10.0	13.0	14.0	15.0	10.0	11.0	5.0	3.0	3.5	.5	.5	.5				
May 19	305			.2							.2			.5	1.0	2.0	5.5	10.0	7.0	13.0	17.0	12.0	16.0	10.0	5.0	.2		.2
Jul. 11	625										.2	.5	.2	.5	.5	1.0	5.0	10.0	16.0	24.0	20.0	12.0	5.0	3.0	1.0	.5	.5	.7
Jul. 22	189															2.0	8.0	15.0	27.0	18.0	19.0	9.0	.5	1.5				
Aug. 7	121															2.0	5.5	9.0	9.0	11.5	6.5	10.5	16.0	10.0	13.0	6.0	2.0	
Sep. 5	478	7.0	17.0	32.0	11.0	10.0	7.5	6.0	2.0	1.5	2.0	1.0	2.0	.2	.2		.2		.2		.2			.2				
Oct. 27	145	1.0	1.0	19.5	30.0	25.0	13.0	2.0	4.0	.5	3.0	1.0																
Nov. 18	36	6.0	28.0	6.0	6.0	6.0	16.0	16.0	3.0	5.0	5.0	3.0																

(of the type commonly used locally for commercial catches (see Viosca, '39)) and dip-nets. Later in the summer, when the water-table of the marshes and shallow ponds fell below the marsh-floor, it was possible to collect only when the marshes and ponds were flooded by heavy rainfalls, after which it was an easy matter to pick up the crawfishes migrating over road-banks and levees at night. This method was used for the remainder of the summer, supplemented of course, by the usual dip-net samples in all standing water to check for the first appearance of the young.

All except two collections were treated statistically following preservation, the exceptions being measured while alive. The cephalothorax length, sex and form (if male) were the data gathered, other notes as necessary also being taken.

The data of each population sample were recorded in table I by reducing the measurements to 2 mm. size classes (those from 10 to 11.9 mm. were counted in the 11 mm. class, for example) and computing the percentage of the collection which each size class represented.

In an attempt to obtain information about particular individuals under natural conditions small celluloid discs, which have been used in shrimp investigations by the U. S. Bureau of Fisheries, were used as tags. The crawfishes thus tagged were kept in shallow concrete tanks (6′ × 6′ × 10″) from which they were frequently recovered by means of an inner tray of quarter-inch-mesh hardware cloth. A few notes on molting and molt-increment were gathered, but the method was not found satisfactory under conditions of close confinement since newly molted crawfishes too readily fell prey to the others.

Gonads from both sexes were dissected out whole from several living crawfishes from the routine collections and sectioned following standard histological procedure.

Seasonal Changes in the Condition of the Testes, and Copulation.—From study of spermatogenesis during the year and observations of copulation in the field and laboratory, it can be stated tentatively that copulation of *C. clarkii* may occur whenever mature males (form I) and females come together in shallow warm water. Since this combination of conditions is present most frequently in nature in July, August, September and October, natural copulation seems for the most part restricted to the fall of the year. Copulation was also observed in the laboratory in January and May.

Except in the later part of February and the first two weeks of March, mature spermatozoa were always found present in the tubules or in the vasa deferentia. The tubules progressively lost their mature sperm in the fall and winter until late February when no sperm were available. At this time mitotic figures were most abundant in the germ cells, and by late March active spermatozoa were again found in the tubules. The vasa deferentia were choked full of spermatozoa in June, July, August and September when the testes were also much larger than at any other time of the year—this being the natural time for copulation as already noted.

Fasten ('14) recorded that the males of *Faxonius virillis* in Wisconsin discharged spermatozoa twice each year, the first through April and May, and the second through September and October, while motile spermatozoa completely filled the tubules only in July, when the testes attained their maximum size.

Two forms of spermatozoa were found in *clarkii.* The one which has four rediating arms was by far the most abundant, and the other, a form with five arms, was not uncommon.

Ovarian Eggs.—The ovaries of females in the summer collections were dissected out and the average size of the eggs in each ovary measured to the nearest 0.1 mm. These figures (table II) showed that the eggs in the ovaries of the individual females developed at varying rates. These rates progressed in a rather orderly rhythm. In May the eggs in nearly

TABLE II. *Maturation of ovarian eggs of C. Clarkii*

Date of Collection	Number of ♀♀ in Collection	Percentage of Size Groups in Collection (Diameter of Eggs in Millimeters)										
		.2	.4	.6	.8	1.0	1.2	1.4	1.6	1.8	2.0	2.2
May 19	30	30	60	10								
July 11	48			2	4	24	8	20	12	20	6	4
July 22	75			2	6	21	10	14	20	20	5	2
Aug. 7	26				2	2	2	18	28	24	24	

all of the ovaries were of the same size, ranging from 0.2 to 0.6 mm. in diameter.

Crawfishes were in burrows in June and extremely hard to collect in significant numbers. From the few collected, however, there was noted an indication of the beginning of differential development in late June. A few of the larger females were found with 1.8 mm. diameter eggs; however, the majority still contained eggs of about 0.4 mm. in diameter.

In July there were three significant groups ranging around 1.0, 1.4 and 1.8 mm. in diameter; and, in early August, nearly all of the eggs were larger than 1.6 mm. diameter, and the greatest numbers of females carrying eggs were found in August and September.

With the increase in diameter of the ovarian eggs, there was a corresponding deepening of color, until the eggs which were light yellow in May became a chocolate-brown in July and August, and filled most of the cavity of the thorax. The eggs were black when laid. Those measured after extrusion were 1.9 mm. to 2.1 mm. (average 2.0 mm.) in diameter.

Season of Egg Laying.—In the Chalmette area thousands of crawfishes were observed "in berry" and with first or second instar young during the latter part of August and the first part of September, 1939. Most of these were in the open water, but some were in burrows. In shallower areas, as along the Industrial Canal in New Orleans, many ovigerous females were in burrows but left them temporarily during heavy rainstorms. Collections made in July, August and September, 1939 showed the majority of the females ovigerous in later August and early September, although some were observed in 1940 spawning as early as late June and as late as October.

Erratic spawnings have been observed from time to time, especially in the rather static ecological conditions of the Audubon Park lagoon in New Orleans. In May, 1939, during a heavy rainstorm of a week's duration, large mature *clarkii* were found migrating from the lagoon to the wet grass on its banks. Large numbers of these died at the edge of the lagoon (these were mostly females) and several which had third-instar young clinging to the abdominal appendages were caught. From the same body of water, several large ovigerous females were collected as late as November 29th, and several others bearing third-instar young, December 13th. It is the writer's belief that the occasional early and late erratic spawnings as the above make little or no change in the gross populations.

Tentatively it may be stated, therefore, that egg-laying occurs for the most part in the estivo-autumnal period, i.e., in the months of June, July, August, September and October, and that the erratic cases of spawning which occur at least in May and December have little or no effect on the gross population of *C. clarkii* in southeastern Louisiana.

Fecundity of the Females.—The number of eggs produced by crawfishes has previously been recorded by Van Deventer ('37) who estimated the numbers of eggs borne on the pleopods of several female

TABLE III. *Ovarian egg production of C. Clarkii*

Cephalo-thorax Length in Mm.	Numbers of Eggs of Individual Females	Total Number Females of Size Class	Total Number Eggs of Class	Average Number Eggs per Female
31	81	1	81	81
32	172 174	2	346	173
33	197	1	197	197
34	141 187 217	3	545	182
35	158 169 178 181 186 194 211 216 238 294	10	2025	202
36	168 194 194 231 235 261 279 362 398	9	2322	258
37	140 193 200 211 212 221 228 241 288	9	1934	215
38	215 222 222 236 245 246 256 258 262 263 268 277 302 302 310 320 345 411	18	4960	275
39	225 227 241 245 272 272 280 284 308 314 352 355 358 363 442	15	4511	301
40	221 250 268 288 293 311 339 356 357 366 379 391 395,398 424	15	5036	336
41	246 260 277 283 285 297 331 348 396 410 518	11	3651	332
42	233 250 309 328 337 376 397 418 419 465 476 600	12	4608	384
43	276 287 291 307 336 342 409	7	2248	321
44	311 311 344 410 428 497 524 616	8	3441	430
45	330 417 694	3	1441	480
46	351 483 541	3	1375	458
47	502	1	502	502
48	495 524	2	1019	505
49	510 753	2	1263	631
50	534	1	534	534
51	556	1	556	556
52	652	1	652	652
	Grand Total	135	43247	313

C. propinquus, and by Tack ('41) who made counts of the eggs of 37 females *C. immunis.* Because of the ease with which the eggs of crawfishes may become disconnected from the pleopods, errors in counts of extruded eggs are more likely to occur from accidental causes than in counts of ovarian eggs.

Accordingly, the ovarian eggs of 135 female *C. clarkii* collected during the summer months were dissected out and counted. In table III the production of eggs of these females is presented. The numbers for the larger and smaller females of the series are of little value at present until more data can be collected so that the averages will be supported by larger numbers; however, the whole series serves to give an indication of the egg production of *C. clarkii.* From the figures of table III it has been concluded that the numbers of eggs produced by female *clarkii* vary in direct proportion to the size of the individual.

Eleven ovigerous females caught on September 23rd were confined in individual bowls until October 11th when all their eggs had hatched and the young were free-swimming. The young from each female were then counted. The number of young per female (table IV)

TABLE IV. *The number of attached young of female C. Clarkii*

Cephalo-thorax Length in Mm.	Number of Young	Average No. of Ovarian Eggs per Females of Same Size Group
35.0	148	202
36.0	135	258
37.0	130	215
39.0	261	301
40.0	167	336
42.0	140, 256, 271, 480	384
46.0	478	458

was somewhat lower than the average numbers of ovarian eggs of the same length classes. It is possible that a greater number of eggs may be developed in the ovary than are laid, since in four females which laid eggs after three months of confinement, some of the mature-sized eggs were retained in the ovary (table V). This may possibly have been induced by an unfavorable environment, because all ovigerous females in the field collections showed degenerate ovaries from which all eggs of mature size had been extruded.

TABLE V. *The number of eggs retained in the ovaries of C. Clarkii laying eggs in confinement*

Cephalothorax Length in Mm.	Number of Eggs Laid	Number of Eggs Retained in Ovary	Total No. of Eggs per Female
33.5	146	2	148
36.0	121	20	141
36.5	241	12	253
37.5	141	10	151

There is also the more likely possibility that there is a mortality to the eggs resulting from either partial fertilization or failure to attach them securely to the swimmerets at the time they are extruded. From these facts it may be argued, therefore, that while a count of the ovarian eggs gives the net possible productivity of the species, only a count of the attached eggs and young compared with the ovarian egg counts can give an estimate of the net productive potentialities, and incidently also an estimate of the mortality rate of eggs and attached young.

The Earliest Young.—From several females confined in laboratory aquaria, the duration of incubation was found to extend over about 14 days, which corresponds to Viosca's ('39) statement that hatching occurs fifteen days after the eggs are laid.

Under natural conditions, the young crawfishes have little chance to return to the parent after they reach the age and size of independence, generally conceded to be after the third instar. Among females confined in laboratory aquaria it was noted that the young crawfishes may be carried for as long as 27 days, but usually were ready for independent existence five days after hatching occurred. Toward the end of this time some of the young had molted at least once more and still returned to cling to the female. The adult was not observed to use any of the young for food during the whole 27-day period.

The second molt usually occurs on the fifth day after hatching. Five day old crawfish (3rd instar) have all of the appendages which are necessary for an independent existence, only the first and sixth pairs of pleopods not yet having been formed. Several of the young crawfishes which were separated from the female the fifth day after hatching were observed to feed regularly and several molted after a few days. The first two instars of *clarkii* have been carefully described and figured by Andrews ('07).

The young appeared in large numbers among the free-swimming population beginning in August, and continued through September, October and November. At the time of their first appearance in the quantitative collections, the young measured from 4 to 6 mm. cephalothorax length, which is equivalent to a total length of from 8 to 12 mm. The smaller crawfishes (less than 15 mm. cephalothorax length) which can be found in limited numbers at practically any time of the year, apparently represent the results of a combination of erratic spawnings and differential growth rates of the young hatched at the normal time.

It may be permissible to conjecture at this point as to the reason why certain members of the adult female population spawn at erratic times. If it is considered that these "ever-present" young grow at differential rates, they must mature at odd times of the year in small numbers, and then it may be considered just as logically that they spawn at correspondingly erratic dates. Especially is this so when it is remembered that copulation *can take place* at any time of the year.

In spite of the long spawning period extending through four months, it is probable that each female carries no more than one brood in any year. Females dissected four months after having spawned in laboratory aquaria were found with small ovaries in the process of regeneration of ova, and the ovaries of females dissected at various times during the year showed that proliferation accelerated in the spring, that is, during May and June. The initiation of the long spawning period is probably dependent on local conditions affecting the hydro-period, or a combination of the rainfall and temperature factors. From local temperature and rainfall records (figure 3) it was seen that the optimum conditions of high temperature and high rainfall occurred in 1940 during the four months of the estival and autumnal periods in which the majority of spawning occurred.

Ecdysis. Signs of Molting.—Molting of all size crawfishes can be predicted from one to three days in advance with a fair degree of accuracy. As the crawfish grows beyond the limits of its hardened exoskeleton a white "waist" appears between the cephalothorax and the abdomen (this stage is termed the "buster"). Molting usually occurs shortly thereafter. For example, seven tagged crawfish which showed the buster appearance one morning were segregated in an open tank. One molted that night, two the next night, and the remainder the third night.

Chidester ('12) referring to *Cambarus bartonius* wrote that he found that two or three days before molting the adult crawfishes came up into the shallow water, exposing their carapaces and drying them thoroughly. By this preliminary drying out Chidester claimed he could predict the approximate time of the molt. More recently, Brown and Cunningham ('39) studying *C. immunis* noted that the approach of molt was usually indicated by a visible separation between the carapace and the first abdominal tergite.

When crawfishes were ready to molt they apparently sought the comparative safety offered by the floating vegetation. Here the majority of the "soft-shells" and "busters" in the collections were found.

The percentage of soft-shells in each collection was calculated, but there was practically no correlation between the percentage of soft-shelled individuals and the light conditions prevailing when they were collected. On the other hand, there was an acceleration of molting in February, March and April when the temperature was still moderate (but becoming increasingly warmer), and also when there was more food available. Increase in molting seems, therefore, to correspond to a "growing period" in those months before the temperature has reached its maximum for the year, and before the majority of the crawfish population has reached maturity and ceased growing.

Increment of Growth at Each Molt.—Records were kept of the molt increments of tagged specimens as well as several kept apart in small fish bowls. Unfortunately, the quantity of data thus secured was not very great, records of only 59 actual molt increments having been accumulated in two years. As may be expected, while the increment per molt was roughly the same throughout all the size-groups, the percentage increase varied inversely with the size of the crawfishes. The average increase in cephalothorax length of all sizes was found to be 2.6 mm. per molt. This figure could easily be used in the formula set forth by Van Deventer ('37) if it were desired to calculate the number of molts through which any size group had passed.

Growth of the Juvenile Population.—During the fall and winter, due to the long period of egg-laying, several size groups probably representing different dates of spawning, appeared in the population. In table I, which represents all of the growth rate data of the population

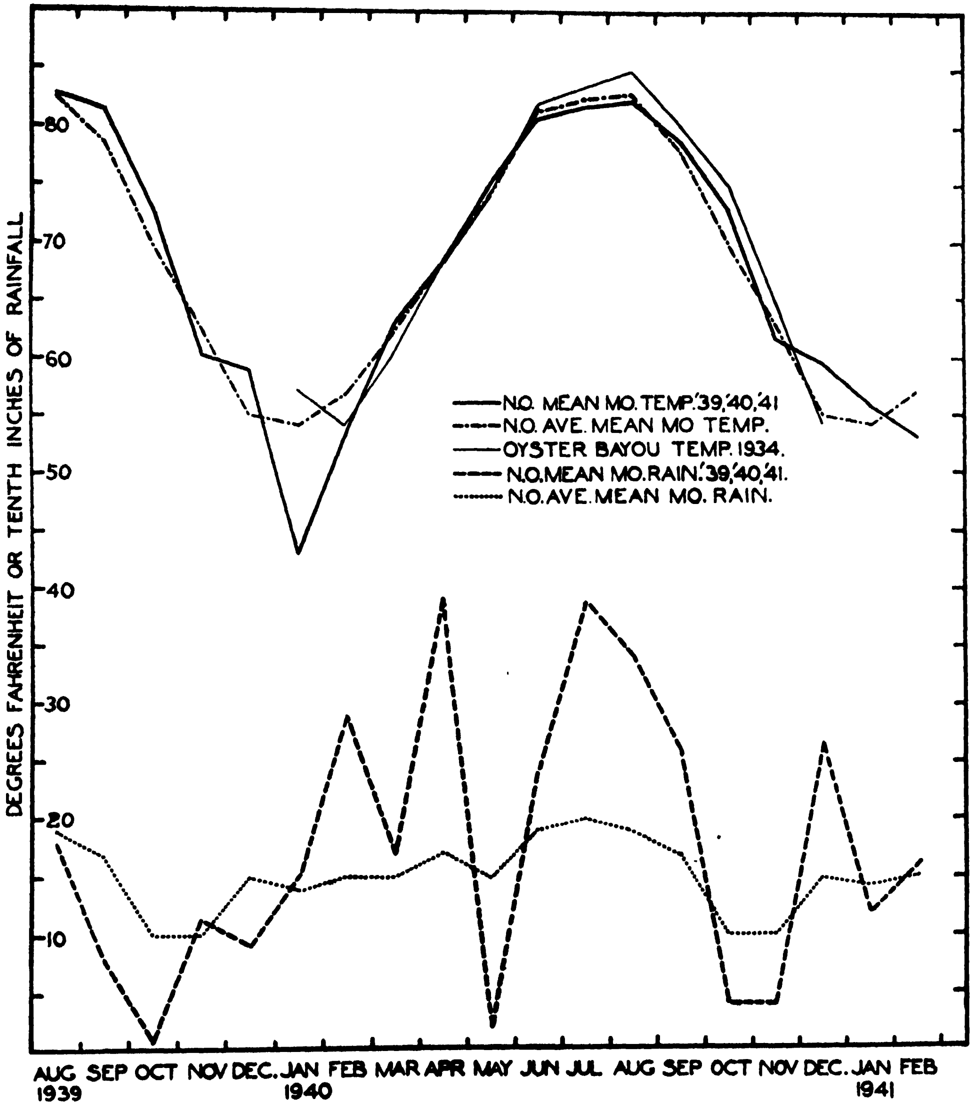

Fig. 3. Graph of temperature and rainfall records in the vicinity of New Orleans, and water temperature records at Oyster Bayou, La., in 1934. Note the conformity of air and water temperatures from the same general vicinity.

samples, certain figures which to the writer seemed to indicate modes are set in heavy type. Some of the figures can be connected by oblique lines to indicate rather constant growth rates, but breaks and inconsistencies in these and other lines occur throughout and somewhat confuse the interpretation of the data. Therefore, it seems wise at present to limit the analysis of the growth of the juvenile populations to certain self-evident observations.

It is significant that several size groups seem to hold throughout the series of figures, apparently representing concentrations of spawning at certain undetermined optimum spawning dates. This observation received corroboration in the data already presented in the section on growth of ovarian eggs at different rates.

By late February and March in 1940 the optimum conditions of growth were attained and the whole population grew at a rapid rate, reaching edible size (approximately 30 mm. cephalothorax length) in April. In May, June and July the population consisted mainly of adults of the 35 mm. and larger size classes. These adults probably came mostly from the slower developing late fall hatchings (late November and December).

Development of the First Pair of Pleopods.—The first pair of pleopods are the last appendages to appear. In both sexes they appear as very small (0.05 mm.) "knob-like" processes on the ventral transverse ridge of the first abdominal somite when the crawfishes are 4.5 mm. cephalothorax length. No sexual dimorphism is apparent at this stage. In the 5.0 mm. group of the males, the first pair of pleopods appears a little larger (0.1 to 0.2) than before, the annulus ventralis of the females appears for the first time and has a straight suture.

As the males increase in length the gonopods (i.e., the first pair of pleopods) retain their simple structure until they appear as 0.4 mm. finger-like processes in the 7.0–7.5 mm. sizes. In the same size-classes the first pair of pleopods of the females increase only slightly in length, not exceeding 0.075 mm.

In the 8.0–8.5 mm. and 9.0–9.5 mm. classes the gonopods flatten out laterally and the length increases, the tip dividing into blunt points. This is when they first assume the structure and appearance of form II appendages. This structure then changes little, except in size, until the animal attains sexual maturity.

There seems little doubt that by gradual growth and differentiation in the early stages the first pair of pleopods of the very small males develop into the form II gonopods of larger immature males, finally assuming the horniness of form I when the crawfishes become sexually mature.

Attainment of Sexual Maturity. Time of Change of Males to First Form.—Until the first part of May young males from eggs laid in the previous year were all of form II.[5] In the April 21st collection, for example, all of the males were of form II except a very few which were of the 40 mm. and larger size-classes. Apparently these larger males of form I represent the few which were immature at the end of the previous autumnal spawning season, and which, in this collection, are in their second year. In the May 19th collection about half of the males were in each of the forms, the larger ones (37 mm. and above) tended to outnumber the second forms in their respective classes, although the second forms were found up through the 53 mm. size-groups (fig. 4). In the July 11th collection, however, all males were of form I except a few of the smaller ones, and by July 22nd, and the rest of the fall all of the males except a very few were of form I.

From these data it is apparent that Creaser's ('33) contention that the maximum percentage of first form males occurs during the breeding season is borne out by *C. clarkii* in Louisiana as well as *C. propinquus* in Michigan.

Size of Males at Sexual Maturity.—Sections of the testes of small, form II males (ranging as low as 20 mm. cephalothorax size-classes) showed mature spermatozoa in the tubules, although it is probable that such individuals, without the presence of effectual means for transferring the spermatozoa to the females, are sexually impotent and must be regarded as immature of juvenile forms. Apparently, therefore, in *C. clarkii* the form of the gonopod *must* be taken as the criterion of sexual maturity of the males. If the crawfishes are examined early in the year, the form II males may be larger than the form I males (figure 4), thus introducing

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[5] Hagen (1870), Faxon (1885), Creaser (1933), etc., have all discussed the relations of the forms of crawfishes to sexual maturity, with partial explanations.

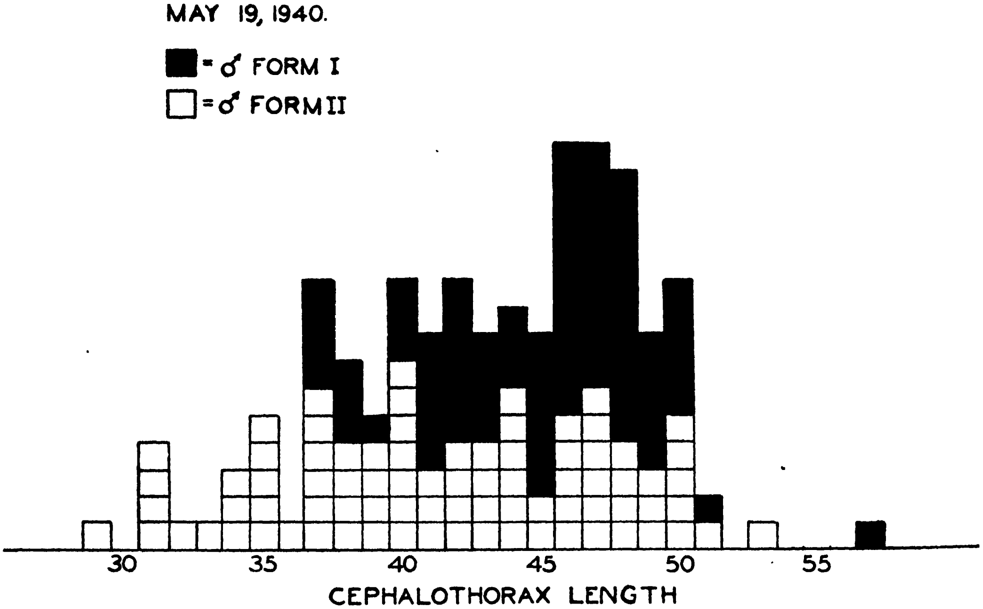

FIG. 4. Graph showing the distribution of form I and form II males in the May 19, 1940, collection. (The ordinate shows numbers of individuals.)

hereditary characteristics and seasonal changes as well as size-groups into the problem. According to these criteria, therefore, only those males which have changed to form I are mature, and the demarcation between mature and immature sizes of males must be set at the lower limit of form I males in the collections. The smallest form I males of *clarkii* were found in the 31 mm. cephalothorax length class in the July 11th collection.

Size of Females at Sexual Maturity.— In the females there is no external morphological criterion by which the attainment of sexual maturity of the year's young females may be ascertained. Accordingly, therefore, the only method of determining the attainment of sexual maturity among the females is by the presence of mature eggs in the ovaries, or by the actual carrying of eggs and young. In the series of ovaries of various sized females collected in May, June, July and August, 1940, it was found that the smallest females with mature eggs were in the 31 mm. size-classes (table III). These smallest, sexually mature females occurred, however, only in the later July and August collections, and many larger females did not contain mature or neary mature eggs in early July. This suggests, as mentioned in regard to the males, that maturation of the females like the males involves changes somewhat similar in physiology, if not in visible aspects, to the changes of the males from form II to form I.

The smallest ovigerous females were in the 35 mm. size-class and were encountered in the September 23rd collection. In the laboratory several females in the 33 mm. size-class from the same collection laid eggs in October. An aberrant female, 30.5 mm. cephalothorax length, carrying young, was collected in the Audubon Park lagoon, New Orleans on March 22, 1941.

Apparently maturity of both males and females of *C. clarkii* can be placed at the attainment of 31–32 mm. cephalothorax length, in addition to the seasonal requirement that the majority of each sex reaches this size at or before the estival period of the year, that is, at the time of the initiation of or during the annual spawning period.

Fall Migration and Death of the Adult Males.—During September 1939, large numbers of males were found migrating by an overland route away from their marsh habitat. Of 750 crawfishes collected crossing a highway at Chalmette, La. in September 1939, only twelve were females, the legions being form I males. The females collected were carrying eggs or young, or gave evidence (dirty pleopods, egg-shell debris, etc.) that their young were already independent.

The males were in very poor condition at the time of this migration. The gills were clogged black with dirt and debris. the hepatic glands were an unhealthy dull gray instead of the normal yellow-orange, the testes appeared degenerate and shrunken, and the crawfishes themselves were very weak and feeble. It is probable that those of this perambulating male population which did not fall prey to some other animal died naturally shortly after the migration began. Viosca ('39) noted their condition as "not fit for human consumption" and wrote of them as moving mostly at night in "armies of tens of thousands." Where they are going or just why they leave the water to begin the migration cannot at present be explained, but it is certain that most of them die at this time of the year. This migration of extraordinary numbers of old males should not be confused with the restless overland wandering of healthy males and ovigerous females which occur after rainstorms in July, August and September, and which have been mentioned previously in this paper.

Not all of the males make the fall death-migration, some few which, along with some of the females, represent slow growth rates and late spawnings and may live over the winter.

The writer believes that the majority of the males which attain sexual maturity in the summer and fall do not live through the winter. Those few males which are collected in the winter and which appear in the early spring probably represent the young which were hatched later in the preceding fall and consequently did not reach form I before the spawning season was culminated, did not mate, and consequently did not become sexually exhausted.

Winter and Early Spring Activities of the Adult Females.—Although undoubtedly large numbers of the spawned females die from various causes in the fall, along with the majority of the adult (form I) perambulating males, large numbers of females (both spawned and not) also undoubtedly over-winter in burrows. These seem to undergo a spring molt which reinvigorates them and prepares them to spawn a second year.

Using the tagging technic, numbers of both sexes collected from among the migrating adults were observed in captivity through November and December, 1939. All of the males died in November. The females, though not much more active than the males, lived through December and part of January, when they were killed by a sudden freeze.

Again, in September 1940, a number of form I males and large females, which had been ovigerous in August, were confined in separate fish bowls in the laboratory. These accepted food in confinement and lived through the fall months under warm conditions. All of the males were in poor condition at the outset, and in November all refused food and died. Nearly all of the females, however, were alive and *had molted once by the end of January, 1941*. When dissected, these females showed normally developing ovaries as compared with females from field collections.

Corroborative evidence that some of the larger immature population of the fall succeeds in over-wintering is the presence of occupied burrows in the marsh and swamp floors (these were especially abundant in the Chalmette, La. area) during the winter; and, also, that the crawfishes of the first spring commercial catches are mostly form II males and a smaller number of females. In a sample of the first commercial catch of 1941, purchased on January 27th, there was one form I male, 61 form II males, and 34 females, all with dirty carapaces and appendages, indicative of a winter burrowing habit. Evidently the males were too young to breed the previous season, and, failing to take part in the migrations, escaped death and were capable of over-wintering in swamp-floor burrows. They were caught in water to which they had probably just returned. Viosca ('31) has already stated that the large over-wintering crawfishes return to the water from their winter burrows in mid-January.

The Relative Abundance of the Sexes.—In an attempt to answer the question of the ratio of the sexes, the numbers of each sex in all the collections were gathered in table VI. The figures fluctuate considerably with the season showing a considerable decrease of females during the warm months (i.e., July, August and September), which may be explained by the habits of the females during that part of the year. It has already been noted that the females are disposed to burrow in these months of the year, during which they reach the culmination of their annual spawning cycle. It is possible that once having burrowed, the females are less disposed to be excited by rising waters and do not leave their burrows in as great numbers as the males, which seem to be brought forthy by every rain, especially at night, during the latter part of the summer.

TABLE VI. *Relative abundance of male and female C. Clarkii at Chalmette and Westwego, Louisiana*

Locality	Month	Total Number	No. of Males (M)	No. of Females (F)	Per Cent of Females to Males (F/M)
Chalmette	1939:				
	October	312	139	173	124.4
	November	161	89	72	80.9
	December	560	270	290	107.4
	1940:				
	January	364	159	206	128.8
	February	740	356	384	107.4
	March	713	330	383	116.0
	April	315	150	165	110.0
	May	305	154	151	98.0
Westwego	July	814	447	367	82.1
	August	121	92	29	32.6
	September	659	330	329	99.7
	October	143	67	76	113.4

The ratios of sexes among the individual size-classes were found to be generally in direct accordance with the composite figure for the collection, which fact also lends support to the belief that the collections were representative of the population in general.

SUMMARY

1. *C. clarkii* is present in Louisiana wherever there are swamps, marshes, lagoons, bayous and sluggish streams except in the piney-woods and brackish coastal marshes. The crawfishes occur in the greatest numbers in shallow, open freshwater marshes, and are most active after dark.

2. Spermatozoa are produced by males almost the year round, being absent only in the latter part of February and early March. Copulation may occur at any time when form I males and mature females come together in shallow warm water.

3. Eggs in the ovaries of individual females mature at varying rates, the first series maturing and being laid in late June and early July, succeeding waves of maturation and laying continuing through August and early September.

4. The number of eggs produced by female *clarkii* at each reproductive period varies in direct proportion to the size of the crawfish.

5. All of the eggs are laid at once, but many are subsequently lost because of failure of fertilization or inadequate attachment to the swimmerets.

6. The eggs hatch in about fourteen days, and then undergo two molts in about five days while still attached to the egg-

cases. After this they become independent.

7. Five-day old (3rd instar) *clarkii* average 5 mm. cephalothorax length.

8. The young crawfish appear in the free-swimming population in large numbers in August and continue to appear through September, October and November.

9. Molting can be predicted by the "buster" appearance which is characterized by a waist of white flesh between the cephalothorax and abdomen.

10. During the fall and winter due to the long period of egg-laying, a number of juvenile size-groups appear in the population. These grow at varying rates throughout the early spring, all attaining edible size (30 mm. cephalothorax length) by May.

11. By gradual growth and differentiation in the early instars the first pair of pleopods of very small males develop into the form II appendages of larger immature males, finally assuming the horniness of form I when the males become sexually mature.

12. Most of the young males from eggs laid in the previous year change from form II to form I from May through July, when nearly all have changed to form I. Regardless of size attained, none of these males changes to form I before May.

13. The attainment of maturity of both males and females of *clarkii* occurs at the inception and during the annual spawning period (during the estival season) when the crawfishes are 31–32 mm. cephalothorax length, or larger.

14. Most of the adult (form I) males spawn in the autumnal season and migrate by the thousands from the swamps and marshes. Apparently all of these males are sexually exhausted and die either as prey to other animals or of old age.

15. Many of the females after spawning participate in the fall migration with the males and die, but many others may over-winter in burrows in the marsh and swamp floors.

16. Crawfishes which over-winter in burrows emerge in January molt once within a few days, the over-wintering males in all probability changing then from form II to form I.

17. There is a decrease in the number of females in the collections in the warmer months (June, July, August) probably because of their disposition to burrow at this time of the year. The ratio of females to males computed for the entire year, however, is approximately 1.00.

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FACTORS INFLUENCING THE NATURAL RESTOCKING OF HIGH ALTITUDE BURNS BY CONIFEROUS TREES IN THE CENTRAL ROCKY MOUNTAINS

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Coniferous forests on approximately three million acres at the higher altitudes in the central Rocky Mountains have been destroyed by forest fires. On much of this area the restoration of the forest by succession is so slow that a serious problem in land management is created. In order to understand this problem more fully and to develop procedures leading to its solution, the Forest Service undertook to study the rate of restocking on the burned-over areas and the factors associated with it. In this study eight typical burns located in Colorado and southern Wyoming between the elevations of 9,000 and 11,000 feet were examined in detail. The data collected during the examination of these areas are presented and interpreted in the following discussion.

Scope of Study

The eight areas studied are located in the Engelmann spruce-alpine fir type, which forms the climax in the subalpine zone (Weaver and Clements, '38) in Colorado and southern Wyoming (figure 1). They cover an area of approximately 100 square miles. All are located in Colorado with the exception of the Libby Flat area on the Medicine Bow National Forest, near the southern border of Wyoming. Pertinent data indicating the location, altitudinal range, major subclimax, soil type, and date of each burn are summarized in table I.

Fires destroyed the forest cover on all areas between 1860 and 1892, more than 50 years prior to the time of this study. Because of them and other destructive processes, various subclimax associations originating through secondary succession have replaced the climax on large areas. The most prominent of these are the Carex-Poa association of the subalpine grassland at the higher altitudes and the aspen (*Populus tremuloides* var. ***aurea*** (Tides.) Daniels) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) subclimax as well as the dry park grassland at middle and lower altitudes of the zone.

From the data in table I it is apparent that the relation between subclimax and elevation is not constant for all burns studied. This is the result of the complex topographic features of the central Rocky Mountains which have a profound influence on the climate and therefore greatly affect the ecological significance of altitudinal levels. The lower and upper limits of the subalpine zone lie considerably higher in the southern and central than in the northern part of the region studied (Stahelin, '41).

Soils on all areas are light brown to brown, slightly podsolic. They can be divided into two categories according to their physical condition and parent rock formation: (1) Light textured loams with high gravel content closely associated with decomposed granite; and (2) denser clay loams derived from various parent materials, including shales, limestone, sandstone, breccia, gneiss, and lava.

The principal trends of the secondary successions in progress on areas studied as well as elsewhere throughout the subalpine forests of the central Rocky Mountains are shown schematically in figure 2. The development of an individual area is strongly influenced by the severity of the fire as well as by the character of the

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[1] Maintained at Fort Collins, Colorado, by the Forest Service, U. S. Department of Agriculture, in cooperation with Colorado State College of Agriculture and Mechanics Arts.

Acknowledgment is made for assistance in computations by W.P.A. Project No. 4294.

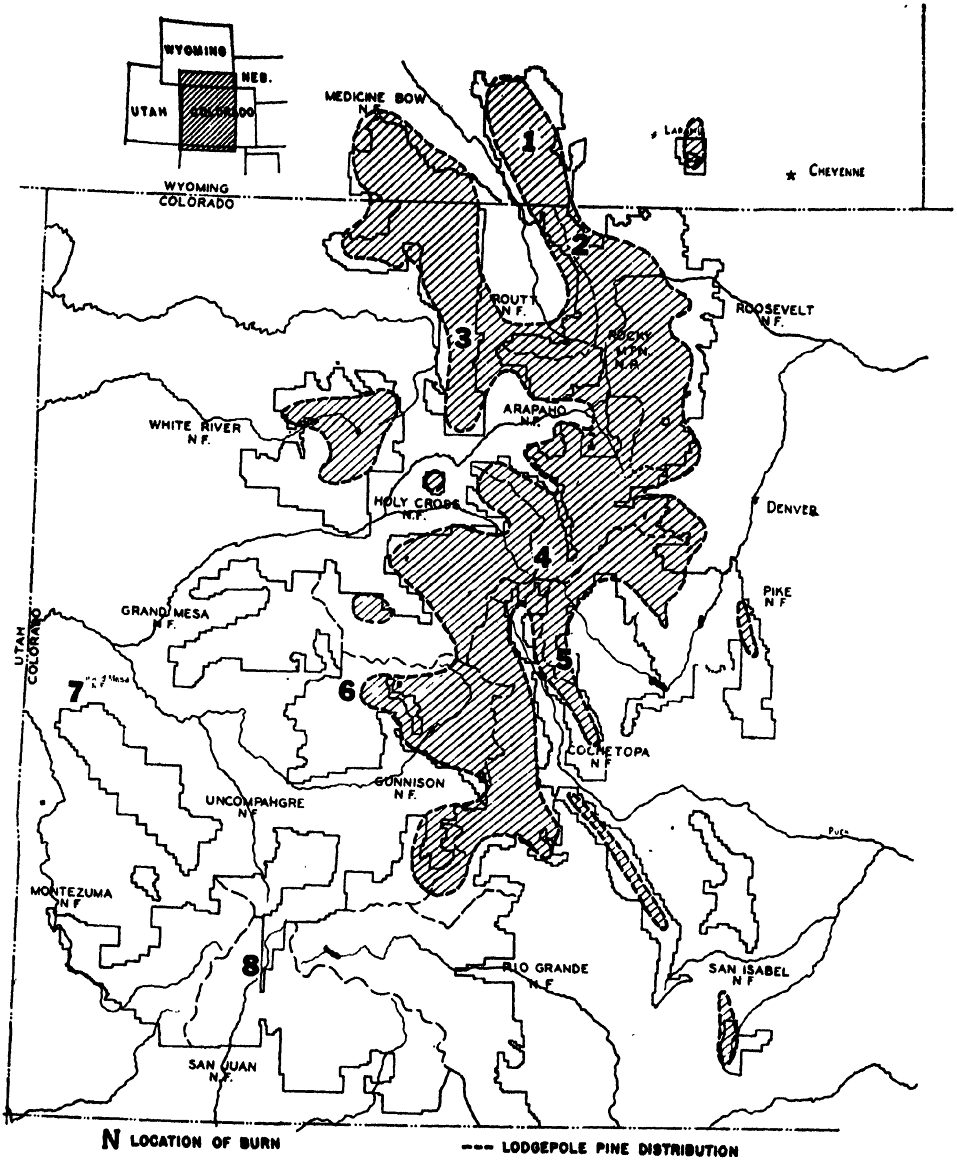

Fig. 1. Location of the burns studied and distribution of lodgepole pine in central Rocky Mountains.

original forest cover, all of which results in complex variations of the trends, as outlined in this diagram. On most of the areas the forest cover prior to the last burn was interspersed with aspen and lodgepole pine as well as open, grass-covered parks. This composition of the forest prior to its destruction determines to a great extent, of course, the resulting secondary succession and subclimax. Within its geographic and altitudinal distribution lodgepole pine formed the dominant subclimax on all areas. It invades and replaces aspen where both species are

TABLE I. *Location, elevation, prevailing subclimax, soil, and date of last forest fire of the burns examined*

No.	Burn	Elevation	Subclimax	Soil	Date of burn
		Feet			
1	Libby Flat	10,500–10,800	Subalpine grass	Non-granitic	1880
2	McIntyre (a)	9,000– 9,500	Lodgepole pine	Granitic	1882
	McIntyre (b)	10,000–10,500	Subalpine grass	Granitic	1882
3	Rabbit Ears	9,800–10,300	Subalpine grass	Non-granitic	1885
4	West Ten Mile (a)	10,000–10,500	Lodgepole pine	Granitic and	1892
	West Ten Mile (b)	10,500–11,000	Subalpine grass	Non-granitic	1892
5	Tumble Creek	9,800–10,200	Lodgepole pine	Non-granitic	1880
6	Ruby Anthracite	9,000– 9,600	Aspen	Non-granitic	1880
7	Fruita	9,000– 9,200	Aspen	Non-granitic	1860
8	Lime Creek (a)	9,500–10,000	Aspen	Non-granitic	1875
	Lime Creek (b)	10,000–10,500	Subalpine grass	Non-granitic	1875

present. Outside of the distribution of lodgepole pine, aspen constitutes the dominant subclimax at lower elevations and subalpine grassland at higher elevations within the subalpine zone. The occurrence of the dry park grassland is restricted mainly to dry sites at lower elevations.

METHODS

Field

This study was a fact-finding survey in which the occurrence of coniferous reproduction was observed in relation to various environmental factors. Each burn selected for study was divided into several strata, which were examined along traverse lines established on contours. The samples were taken on a milacre basis. Forest reproduction (all trees less than 3.5 inches in diameter at breast height) was recorded by species for each milacre according to the stocked-quadrat method (Haig, '31). Groups of 20, 10, or occasionally only 5 consecutive milacres were located mechanically along the traverse lines, the number of milacres in each group depending on the uniformity of the

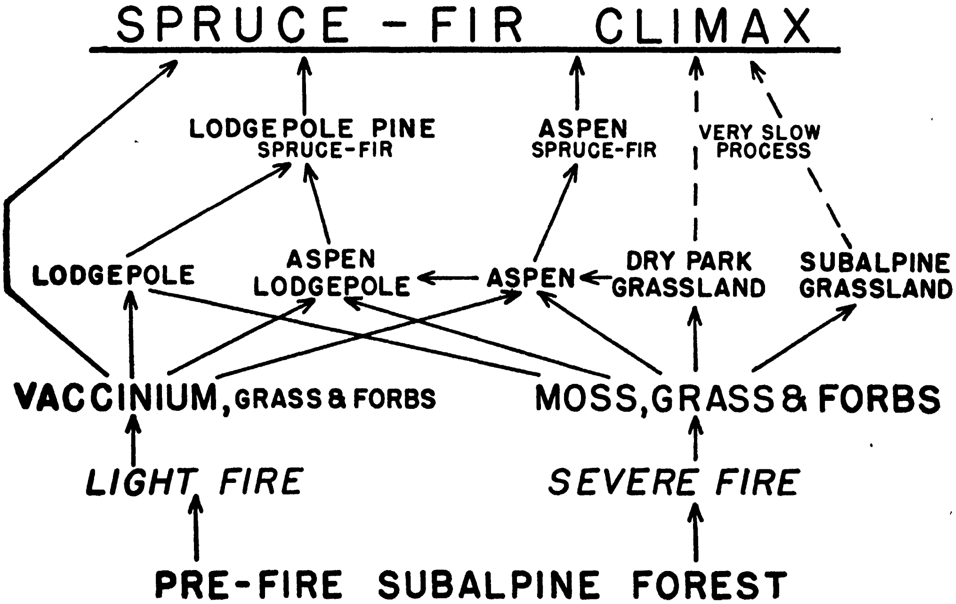

FIG. 2. Major trends of secondary succession in subalpine forest after light and severe forest fires.

environmental factors. Descriptive notes were taken for each group of milacres on exposure, percentage of slope, topographic position, soil characteristics and rock formation, depth of litter and humus, composition and density of ground vegetation, abundance of slash left from fire, degree and kind of grazing, and rodent activity. A tally was made by species of diameter classes of all seed trees within one and two chains of the traverse lines.

Classification of Field Data

Based on a detailed analysis of the field data, the following classification of the principal factors affecting the rate of coniferous restocking was chosen for the presentation of the results of this study.

Prevailing Subclimax.—All burns were arranged into three broad groups: (1) Areas located within the geographic and altitudinal distribution of lodgepole pine; (2) areas outside of the distribution of lodgepole pine and within the aspen zone; and (3) areas outside of the distribution of lodgepole pine and above the aspen zone. Although lodgepole pine occurs occasionally at or near the timberline, it does not form a dominant subclimax in the highest portion of the subalpine zone. The Libby Flat, Rabbit Ears, as well as the upper parts of the McIntyre and West Ten Mile burns (burns No. 1, 3, 2b, and 4b) were therefore classed in the third group.

Seed Trees.—Each plot, consisting of a group of from five to twenty milacres was classified according to abundance and distribution of the seed trees surrounding it. Expressed in number of trees and distance of trees from the traverse line on which the milacre group is located the classes were: (1) Many seed trees—at least five within one chain, or if none within one chain, then at least fifteen within from one to two chains; (2) few seed trees—at least one within two chains, but fewer than specified for class of many seed trees; (3) no seed trees—no seed trees within two chains of traverse lines. All trees with a diameter of more than 5½ inches at breast height were considered seed trees.

Exposure.—All plots were grouped into the four cardinal exposures: north, east, south, and west.

Ground Cover.—All plots were segregated into three broad classes based on plant cover: (1) Grass—all plots not located in aspen or coniferous stands and on which *Vaccinium* spp. contributed less than one-fifth of the total ground vegetation by density. The cover on these plots consisted mostly of sedges, grasses, and forbs, ranging from a very sparse cover to a nearly solid turf in moist meadows; (2) Vaccinium—all plots on which *Vaccinium* spp. furnished one-fifth or more of the total cover by density; (3) Aspen—all plots stocked with aspen regardless of aspen crown density and character of ground vegetation.

Soil.—On the burns studied the occurrence of light textured, gravelly soils and heavier clayey soils was so closely associated with the presence or absence of granitic parent rock that all plots were classified as granitic and non-granitic.

RESULTS

Coniferous Restocking according to Prevailing Subclimax

The location of the burn in respect to the prevailing subclimax association has an important influence on the progress of the coniferous restocking (table II). Within the distribution of lodgepole pine 39 per cent of the milacres had been restocked with coniferous seedlings since the fires which occurred approximately not less than 50 years ago. On the burns located outside of the distribution of lodgepole pine, 8 per cent of the milacres were stocked in the aspen zone, and only 5 per cent above the aspen zone.

These differences in the stocking between the subclimax zones demonstrate that the problem of restoring the coniferous cover on areas where lodgepole pine was absent is much more acute than where lodgepole pine was present in the original

TABLE II. *Coniferous reproduction according to prevailing subclimax association on high altitude burns*

Location of burn	Lodgepole pine	Engelmann spruce	Alpine fir	All species	No. of plots
	Percentage of milacres stocked				
Within distribution of lodgepole pine	33	9	14	39	1,720
Outside distribution of lodgepole pine					
(*a*) in aspen zone	—	4	6	8	2,100
(*b*) above aspen zone	—	4	1	5	3,510

stand. The ability of lodgepole pine seed in cones to escape destruction by severe fires explains in part the better stocking found within the range of lodgepole pine. However, as shown later, the close association of lodgepole pine with light textured soils of high gravel content contributes also directly and indirectly to the higher degree of stocking on these areas. Within the distribution of lodgepole pine, Engelmann spruce and alpine fir compose 9 and 14 per cent of the coniferous reproduction against 33 per cent for lodgepole pine. Since most of the plots stocked by these two species are already occupied by one or more lodgepole pine seedlings, the total percentage of plots stocked was increased by only 6 per cent (from 33 to 39) by including them.

ENVIRONMENTAL FACTORS AND RESTOCKING

Individual Factors.—The rate of the natural coniferous restocking on burned-over areas is not uniform, but depends on the influence of a multitude of interacting factors. Of all the environmental factors recorded in the field, abundance of seed trees, exposure, ground cover, and soil showed the most consistent relation with the rate of restocking. The average degree of stocking in relation to these factors is shown in table III.

The relation between presence of milacres stocked and abundance of seed trees is naturally very close. The data indicate that about ten seed trees per acre (many seed trees) will insure the reestablishment of the coniferous cover within 50 years after the fire. Natural reproduction is best on north and least on south exposures. The difference between east and west exposures is not striking nor is it consistent between the various burns.

The character of the ground cover has an important influence on the density of reproduction. On open areas with similar seed trees and exposure, coniferous reproduction was found to be consistently and materially better on plots with a vaccinium cover (*V. scoparium, V. oreophyllum, V. caespitosum*) than on plots with grass cover. This statement does not imply that

TABLE III. *Coniferous reproduction in relation to abundance of seed trees, exposure, cover, and soil*

Environmental factors	Within distribution of lodgepole pine	Outside distribution of lodgepole pine		All plots	Number of plots
		Aspen zone	Above aspen		
	Percentage of milacres stocked				
Seed trees					
Many	49	24	9	31	2,430
Few	21	6	7	9	2,500
None	0*	1	2	2	2,400
Exposure					
North	65	15	11	35	1,720
West	30	6	8	11	1,550
East	14	9	4	7	1,920
South	13	4	3	5	2,140
Cover					
Vaccinium	65	30*	12	35	1,830
Aspen	19	10	—	15	1,240
Grass	13	6	2	4	4,260
Soil					
Granitic	47	—	9	30	2,110
Non-granitic	20	8	4	7	5,220
Average	39	8	5	14	7,330

* Based on less than 100 milacres.

a vaccinium cover has in itself a beneficial influence. Apparently, however, vaccinium does not prevent seeds from reaching mineral soil to the same extent as a cover of sod-forming herbaceous vegetation, and also it offers less severe competition to the seedlings. When all plots with grass and vaccinium cover were arranged according to the proportionate contribution of vaccinium to the density of the total ground cover, the corresponding percentages of milacres stocked by coniferous trees were: Vaccinium—one-half or more of total ground cover—64 per cent; vaccinium—one-third—36 per cent; vaccinium—one-fourth to one-fifth—17 per cent; average stocking for all vaccinium plots—35 per cent; vaccinium less than one-fifth (grass plots)—4 per cent.

In aspen stands the coniferous restocking was found to be less than on plots supporting vaccinium and higher than in grass cover. No consistent relation could be established between the amount of coniferous reproduction and the crown density of the aspen stand. This may be due to the fact that all burns studied were above the altitudinal optimum for aspen and, therefore, stands too dense for successful invasion by coniferous seedlings were not encountered. The character or composition of ground cover under aspen failed to show any appreciable effect on the degree of coniferous stocking. *Achillea lanulosa, Carex* spp., *Bromus anomalus, Fragaria glauca, Thalictrum fendleri, Vicia americana,* and *Thermopsis montana* are among the principal herbaceous species found under aspen. The mixture of species varies greatly according to soil and density of the aspen stand, but as a rule, the herbaceous cover is light and underbrush is only sparingly present.

Restocking was consistently better on soils derived from granitic than on soils derived from non-granitic parent material on all burns where both soil types are present. The influence of the soil cannot be dissociated, however, from the effect of the cover, as both are closely interrelated. The inhibiting effect of grass on the degree of stocking is less pronounced on granitic soils. The close relation between soil types and ground vegetation is clearly expressed in the different distribution of grass and vaccinium plots on the two soils. Plots with a vaccinium cover outnumber grass plots almost three to one on granitic soils, while grass plots outnumber vaccinium plots about six to one on the non-granitic soils. This soil-cover interrelation is confounded in the average figures for coniferous restocking presented in table III.

Since in this analysis vaccinium and grass represent two broad ground cover classes, the character of the average vaccinium or grass cover is quite different on the two soils. Vaccinium plots on non-granitic soil represent generally a mixture of *Vaccinium* spp. with various grasses and herbs which fall near the border line between the grass and vaccinium cover classification. Grass plots show a lower average density and different species composition on granitic than on non-granitic soils. A dense turf composed of *Carex* spp., *Poa alpina* and associated species, principally *Deschampsia caespitosa, Trisetum spicatum, Festuca ovina, Potentilla* spp., *Phleum alpinum,* and *Taraxacum officinale* is characteristic for open areas on heavier soils at high altitudes. Gravelly granitic soils, on the other hand, bear a more open ground cover in which *Vaccinium scoparium, Arctostaphylos uva-ursi, Antennaria rosea, Fragaria glauca, Achillea lanulosa, Senecio* spp., *Erigeron* spp., *Solidago* spp., and *Pentstemon* spp. play a prominent part. This latter type of ground cover offers less competition to the establishment of seedlings.

Coniferous restocking appears to be related to the porosity of the soil which, in turn, depends on the clay content as well as on the type of vegetation growing on the soil. The infiltration rates for various soil and cover combinations were determined by measuring the amount of water absorbed by the soil in a given time through 4-inch cylinders driven about two inches into the soil. Expressed on a relative basis, with the infiltration rate of grass plots on non-granitic soils equal to one, these rates were: 1.4 for vaccinium, 1.3 for aspen, and 2.2 for virgin forest on non-granitic soils, and 1.5 for grass, 2.5 for vaccinium, 2.7 for aspen, and 2.7 for virgin forest on granitic soils.

Combined Effect of Environmental Factors on Stocking.—Restocking obviously depends on the combined effect produced by all the interrelated influences. Each factor should, therefore, be considered in connection with the general setting in which it operates. This interrelationship is indicated in table IV where the percentage of milacres stocked for all combinations of the three environmental factors, seed trees, exposure, and vegetation are presented. The environmental factor combinations are arranged according to degree to which they seem associated with percentage of milacres stocked by seedlings. The position of the various factors in the array of combinations gives a good indication of their relative influence. The factor-combinations shown in this table are combined into three broad groups, representing favorable, unfavorable, and very unfavorable conditions for natural restocking.

Many seed trees, north exposures, and vaccinium predominate in the favorable group, while no seed trees, south exposures, and grass prevail in the very unfavorable group. Since the effect of exposure is largely equalized under an aspen cover the stocking in relation to different exposures is not presented separately.

The average degree of restocking depends primarily on whether or not factor combinations favorable or unfavorable to the establishment of coniferous reproduction predominate on a given area. In table IV the proportion of plots affected by favorable factor combinations is shown to be much greater on burns inside than outside of the distribution of lodgepole pine. Within the distribution of lodgepole pine, plots with a vaccinium cover and many surrounding seed trees are more numerous than plots with grass cover and no seed trees, while outside the distribution of lodgepole pine the reverse is true. This specific distribution of number of seed trees and character of ground cover is not haphazard, but very characteristic for the different burns. Only the relative representation of the different exposure classes is largely accidental, since it depends on the physiography of the drainages selected for this study. The greater abundance of seed trees on burns within the lodgepole pine zone holds true mainly for lodgepole pine and to a lesser degree only for spruce and fir. Most of the lodgepole pine seed trees examined originated immediately after the fires and were now of sufficient size to produce seed. Spruce and fir seed trees were about equally scarce on all three groups of burns. They were, with few exceptions, older than the pine and confined to such locations as draws, ridges, or wet depressions which escaped the most intense heat of the fire.

The fact that more than two-thirds of the plots within the lodgepole pine zone were located on granitic soil contributes also to their superior stocking. The proportion of granitic plots outside the lodgepole pine zone is small and mostly confined to the higher portions of the McIntyre (b) and the West Ten Mile (b) burns at or above the upper altitudinal limit of lodgepole pine. Not only the ground cover after the burn but also the original forest cover is generally much lighter on granitic than on non-granitic soils, and consequently the intensity of a forest fire tends to be less severe. As a result, seed trees are more abundant as a rule on burns on granitic areas and also species typical of the forest floor vegetation are more prominent than species which are aliens to the forest flora. The cumulative effect of all these factors working together results in a much higher rate of stocking on areas located within as compared to areas located outside the distribution of lodgepole pine.

TABLE IV. *Coniferous reproduction in relation to the combined effect of major environmental factors*

Combination of environmental factors			Within distribution of lodgepole pine	Outside distribution of lodgepole pine		Soils		Average all burns	Number of plots
Seed trees	Exposure	Vegetation		Aspen zone	Above aspen	Granitic	Non-granitic		
			Percentage of milacres stocked						
Many	North	Vaccinium	85	80*	30*	91	56	80	490
Many	East & West	Vaccinium	50	—	14	58	10	38	240
Many	North	Grass	30*	40	20*	30*	36	35	130
Few	North	Vaccinium	53	5	19	44	12	29	260
Many	All	Aspen	30	24	—	30	25	28	400
Many	South	Vaccinium	19	—	18	9	32	19	140
Average: Favorable combinations			55	31	19	55	30	45	1,660
Few	All	Aspen	9	21	—	4	19	15	420
Few	North	Grass	36	4	11	28	4	12	400
Few	East & West	Vaccinium	—	—	11	11	†	11	320
Many	East & West	Grass	10*	15	6	†	10	10	590
None	North	Vaccinium	—	—	3	†	3	3	80
None	East & West	Vaccinium	—	—	10	13	6	10	220
Average: Unfavorable combinations			15	13	9	13	10	11	2,030
Many	South	Grass	3	†	5	†	4	4	440
Few	South	Vaccinium	10*	—	0	0	†	2	80
None	South	Vaccinium	—	—	—	—	—	—	0
None	North	Grass	†	2*	2	2	2	2	200
Few	East & West	Grass	†	0.3	1.4	0	0.9	0.8	640
Few	South	Grass	1.7	†	1.7	5	0.9	1.6	380
None	All	Aspen	0	1.4	—	0*	1.3	1.2	420
None	East & West	Grass	—	0	0.5	†	0.3	0.3	910
None	South	Grass	—	0	0.2	†	0.2	0.2	570
Average: Very unfavorable combinations			2	0.6	1.4	1.4	1.2	1.2	3,640
Average			39	8	5	30	7	14	7,330
			Number of milacre plots						
Favorable combinations			1,100	260	300	1,000	660	1,660	
Unfavorable combinations			350	650	1,030	750	1,280	2,030	
Very unfavorable combinations			270	1,190	2,180	360	3,280	3,640	
Total			1,720	2,100	3,510	2,110	5,220	7,330	

* Less than 50 milacre plots. † Less than 25 milacre plots.

SUCCESSIONAL DEVELOPMENT ON BURNS LOCATED WITHIN THE LODGEPOLE PINE ZONE

Special data not presented in the previous section were collected on Jim Creek burn on the Arapaho National Forest. This area, which burned in 1915, illustrates the earlier stage of restocking on granitic soils in the lodgepole pine zone above 9,300 feet. The forest cover before the fire consisted of a spruce-fir stand on north slopes with some lodgepole pine, and a lodgepole pine stand on south slopes in mixture with spruce, fir, and aspen. On the south slope a stand of aspen invaded the greater part of the area after the fire up to an elevation of approximately 10,000 feet. On this burn the area stocked with lodgepole pine was found to be 13 per cent on north slopes and 3 per cent on south slopes, against 2 per cent on north slopes and none on south slopes for Engelmann spruce and alpine fir combined. All spruce and fir seedlings were under three feet in height while 60 per cent of the lodgepole pine seedlings were over three feet. Lodgepole pine seedlings over three feet high originated the year following the fire and at present, after 25 years, are bearing a light cone crop. It can be expected that within another 25 years the Jim Creek area will present the same average degree of stocking as the older burns in the lodgepole pine zone.

The lower north slope portion of the West Ten Mile drainage, burned over in 1892, offers a typical example of the successional status under favorable conditions in the lodgepole pine zone about 50 years after a forest fire. This slope is occupied by an average of 12.5 lodgepole pine and 1.7 spruce and fir to the acre, varying in size from 6 to 10 inches in diameter at breast height. Age determination at the ground line revealed that these trees originated the year after the fire with the exception of a few older spruce and fir trees. From these seed trees an average stocking of at least 410 well-spaced seedlings has developed in recent years. This stocking, expressed in per cent of milacres stocked, corresponds to 29 per cent for lodgepole pine, 16 per cent for Engelmann spruce, 2 per cent for alpine fir, and 41 per cent for all species combined. On the south slope the seed trees are considerably scarcer and the stocking by seedlings averages only 80 per acre.

As these seedlings grow and begin to produce seed, the stocking rate will increase gradually until a complete forest cover is created. The resulting stand will be uneven-aged, with some spruce and fir in mixture with lodgepole pine. With complete protection from future fires, this area will eventually revert to the spruce-fir climax type. Areas on which lodgepole pine established itself in a fully stocked stand immediately after the fire on this burn were very limited.

Gradual re-establishment of the forest cover with uneven-aged stands as a result appears to be the rule rather than the exception in the lodgepole pine zone above 9,000 feet in the central Rocky Mountains. This statement does not imply that extensive even-aged stands of lodgepole pine do not occur in the region, especially near the lower limits of the subalpine zone. The conditions leading to rapid and complete restocking of burns with lodgepole pine have been reported in detail by Clements ('10) for a series of burns in the Estes Park basin of Colorado.

SUCCESSIONAL DEVELOPMENT ON BURNS LOCATED OUTSIDE THE DISTRIBUTION OF LODGEPOLE PINE

On burns located outside the distribution of lodgepole pine, a rapid re-establishment of the coniferous cover is confined to areas where, because of the low intensity of the fire, many trees escaped severe damage and the forest soil and its vegetation was not greatly changed. These conditions are restricted mostly to the edges and "unscarred islands" within the burn. In the major portion of the burned-over areas a new sere is initiated by the fire.

Where aspen was present in the original stand it will tend, through root suckers, to monopolize all areas which conform to its site requirements. Evidence of aspen stands originating from seed was not found on any burns examined. On most areas inside the aspen subclimax zone, aspen was only very sparingly represented in the original stand, and often completely absent, especially on north exposures. As a result, aspen stands alternate with open grassy areas which the aspen are still in the process of invading. Age determinations in seemingly even-aged aspen stands revealed a remarkable variation which proves their gradual establishment by spreading from the root stocks of single trees or colonies of aspen trees which existed prior to the fire. The proportion of aspen areas on the burns decreases rapidly toward the upper altitudinal limit of aspen.

The effect of aspen in the process of the re-establishment of a coniferous forest is to prevent the development of a dense herbaceous ground cover, or to reverse this development where grasses have already invaded the ground, and thus keep the area open for coniferous reproduction. Aspen stands, if not too dense, create a favorable environment for the re-establishment of the spruce and fir climax species. However, where the seed supply is insufficient, the rate at which coniferous species invade an aspen stand is extremely slow, as demonstrated by the low degree of stocking for the factor-combination class of no seed trees and aspen which ranks near the bottom of table IV.

Open areas occupied by turf-forming species belonging to the Carex-Poa association present by far the least favorable conditions for the establishment of coniferous seedlings. Such a ground cover is found on the largest part of the burned-over areas at the highest altitudes outside of the lodgepole pine zone. In the first decades after the fire, decaying tree trunks impede to some extent the spread of the herbaceous vegetation and offer at the same time a favorable medium for seedling establishment. As disintegration progresses this influence disappears. Where the coniferous species have not

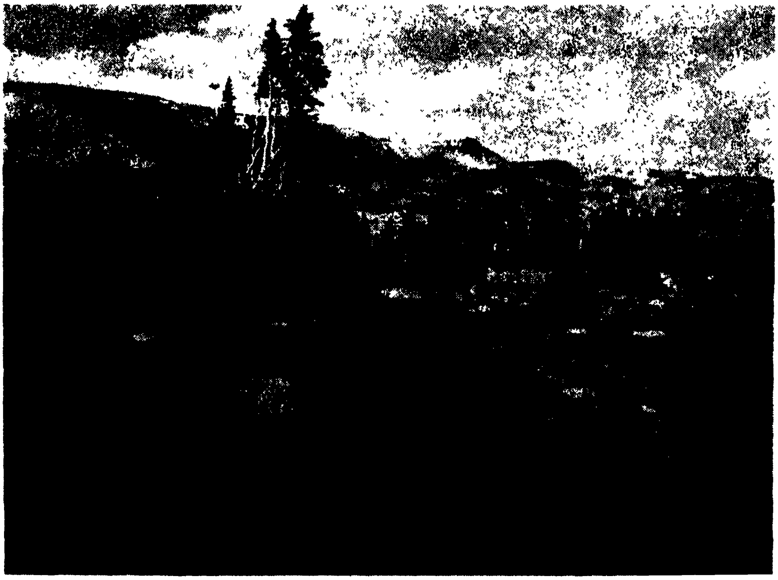

FIG. 3. High altitude burn on the Libby Flat. The sod formed by herbaceous species of the Carex-Poa association creates an effective barrier to the re-establishment of the spruce.

been able to establish themselves sufficiently in the meantime, the Carex-Poa subclimax will take a long lease on the area and will erect a very effective successional barrier (figure 3). The restoration of the coniferous forest can be achieved practically only by artificial reforestation on such areas.

SUMMARY AND CONCLUSIONS

A survey was conducted to determine the status of natural coniferous regeneration on burned over areas located in the subalpine forest zone of the central Rocky Mountains. Eight areas, ranging in elevation from 9,000 to 11,000 feet and located on eight national forests in Colorado and southern Wyoming were examined. The last major forest fire occurred on these areas from 50 to 70 years prior to this examination. The conditions studied are representative of approximately three million acres of burned-over lands in the Engelmann spruce-alpine fir type in these two states.

The sudden destruction of the climax association by forest fires gives rise to the establishment of a fire subclimax of the aspen and lodgepole pine as well as to the invasion by plants of the Carex-Poa association at the higher and by dry park grassland associations at the lower elevations in the subalpine forest zone. The restoration of the coniferous forest cover on these areas is an important problem on the national forests of this region and a thorough knowledge of the natural processes involved is indispensable for its efficient solution.

This survey and analysis of data established the following outstanding facts:

1. The subclimax prevailing in the secondary succession has a strong influence on the rate of the recovery of the coniferous cover. Burns in the subalpine forest zone can be divided into three broad groups: (*a*) burns within the geographic and altitudinal distribution of lodgepole pine; (*b*) burns outside the distribution of lodgepole pine but within the altitudinal distribution of aspen; (*c*) burns located outside and above the distribution of both lodgepole pine and aspen. In each one of these groups the future development is largely determined by the relative abundance of lodgepole pine, aspen, or grass in the original community as a result of the past history.

2. Where lodgepole pine was represented in the original stand, a sufficient number of lodgepole pine seeds escape destruction during forest fires to form eventually a stand of seed trees which will re-establish a lodgepole pine cover on the area within 50 to 100 years. This is true even though aspen or grass becomes temporarily dominant immediately after the fire.

3. Outside of the distribution of lodgepole pine, aspen constitutes the typical fire subclimax at lower elevations in the subalpine forest zone. However, where aspen was not an important component of the original stand, it establishes itself only through the relatively slow process of migration by root suckers against the quickly invading herbaceous species of the dry park grassland communities. Aspen creates a favorable environment for the establishment of spruce and fir seedlings. The rate of coniferous restocking under aspen depends entirely on the presence of seed trees which escaped destruction during the fire.

4. Sedges, grasses, and other species characteristic of the subalpine grassland build up a dense turf on burned-over areas located above the distribution of lodgepole pine and aspen. This sod constitutes an effective barrier to the establishment of coniferous seedlings. Indications are that this herbaceous cover will be able to maintain itself for centuries.

5. The general conditions on burned-over areas are influenced and modified by many interrelated factors. Among the most important factors influencing directly or indirectly the rate of coniferous restocking are abundance of seed trees, exposure, cover, and soil type.

6. According to the restocking observed, the combinations of the major en-

vironmental factors can be grouped into three broad classes: those which are favorable, unfavorable, and very unfavorable, to the establishment of seedlings. Many seed trees, north exposures and a vaccinium cover create favorable conditions; no seed trees, south exposures and a grassy ground cover create very unfavorable conditions for natural restocking. Favorable conditions occur more frequently on the light, gravelly soils commonly associated with granitic rock formations on the areas studied than on the heavier clay and loam soil derived from other parent material.

7. It can be expected, in general, that areas supporting more than ten well-scattered seed trees per acre will revert to a coniferous stand on all sites within 50 years after a forest fire, except when grass is dense. Grassy areas with less than ten seed trees per acre must usually be planted in order to re-establish a coniferous cover.

8. In aspen stands and on open sites where vaccinium forms a major component of the ground cover three to four scattered seed trees per acre are sufficient to insure satisfactory natural coniferous restocking within 50 to 100 years after a forest fire.

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POPULATION STUDIES OF THE ANT, *PRENOLEPIS IMPARIS* SAY[1]

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Studies of population of ants have been scattered and fragmentary, and have for the most part been based upon isolated counts of members of large or otherwise conspicuous colonies. Emerson ('39) has pointed out that "Information on the total population of any social insect per unit of area is very meager and generalizations and comparisons are still bound to rest on inadequate data." This paper attempts to establish quantitative data concerning the population of colonies of the ant *Prenolepis imparis* Say, the characteristic nest structure, the number of colonies in a restricted area, and the amount of territory each colony needs to maintain itself. More specifically its purpose is to determine: (1) the average population both as to total numbers and types of individuals of a *Prenolepis* colony and within what extremes it fluctuates at each season of the year; (2) the standard of nest structure and in what ways nest size correlates with colony size; (3) the density of population of colonies within a given area; (4) how much of the earth's surface is required to support a colony and whether each colony maintains an area which it patrols for food and defends as its own territory against the invasion by members of other nests.

The work had to be carried on at two different places because the writer was at St. Charles, Missouri, during the winter (September to June) and at Tiffin, Ohio, during the summer (June to September). This, however, was not a serious disadvantage, because the ants showed similar habits in the two places.

To determine the population of individuals in a colony 20 nests were dug, 11 at St. Charles and 9 at Tiffin, in order to spread the count throughout the twelve months of the year. Only the St. Charles nests were used in the diagrams which show nest structure, since the clay was stiffer there and consequently galleries and chambers could be more accurately excavated and measured. The number of colonies in a restricted area was counted at St. Charles because only at flight time in early spring are nests conspicuous enough to allow a fairly accurate count. The amount of territory used by individual colonies had to be determined at Tiffin during summer leisure because the study required lengthy daily observations extending over a number of consecutive weeks.

The ant *Prenolepis imparis* was chosen because it is wide-spread and abundant, lives in small well-defined colonies and makes definite (although invisible) odor trails which may be marked and used in determining limits of the foraging area of a colony.

The St. Charles part of the work was done in the orchard of Mr. and Mrs. F. C. Becker, a lot of 108 × 155 feet containing a variety of fruit trees among which apple trees predominate. The grass which covers the ground is kept cut as lawn over the western half but allowed to grow tall over the eastern portion. The soil of the orchard is stiff humus-clay for a depth of 3 to 15 inches; below this, fine, firmly packed yellow clay extends down to hard pan 19 feet below. There are no stones and the clay has never been plowed, so that it is uniformly hard and very solid.

The Tiffin excavations and observations were made in the Talbot back yard, where the ant nests centered around a pear tree in the lawn. Soil here is basically clay but is less heavy and has a much greater mixture of humus than that of St. Charles.

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[1] I am indebted to Dr. C. H. Kennedy and Dr. Thomas Park for helpful suggestions, and to Mr. and Mrs. F. C. Becker for extensive use of their orchard.

Populations of Colonies

Since the colony is the unit of population of any social insect, determination of its size is fundamental. The procedure for making such a study is to dig the nests and capture their entire populations for counting. Furthermore, enough colonies must be secured to establish an average population for each season of the year, since the percentage of eggs, larvae, pupae, workers, males, and females varies enormously from season to season.

Prenolepis nests were dug throughout the year 1940–41, the fall, winter, and spring ones being secured at St. Charles, Missouri, and the summer ones at Tiffin, Ohio. The Tiffin colonies were smaller than those at St. Charles but were otherwise entirely similar in organization. Table I gives a summary of populations of the 20 colonies.

Winter.—Contrary to the habits of many ants, *Prenolepis* does not overwinter any brood, but does maintain males and females in the nest. Thus a winter colony consists of the nest queen, males and females (if it is a mature colony), and workers which are sharply divided into the small dark non-repletes and the light colored, enormously swollen repletes whose function it is to store food for the rest of the colony. *Prenolepis* does not maintain a strict hibernation but forages all during the winter whenever the temperature is high enough for movement (workers appear at the surface of the nest as soon as the temperature rises above freezing and remain active until it lowers to freezing again).

Spring.—*Prenolepis* males and females fly on the first warm days of spring (April 6, 9, and 10 for 1941) and thus leave the colony at its lowest ebb of population, reducing it to the queen and the replete and non-replete workers. After flight there is an almost entire cessation of foraging and all other above ground activity; this lasts into midsummer.

Summer.—This is the time of maturing of brood. Unfortunately no nests could be found at Tiffin in June because of the peculiar lull of activity. However Dennis ('40) reports from Tennessee that eggs are not laid until the beginning of July, and this seemed to be true for the Tiffin colonies. It seems evident that all of the eggs for the year were laid at about the same time, for nests dug July 15 and 16 showed only a few eggs remaining unhatched, and none were found after that. Furthermore all brood was matured at about the same rate. This is quite contrary to the habits of many ants and probably may be accounted for by the presence of repletes which provide a constant and abundant source of food. Larvae reached their height of abundance during the latter part of July and diminished during early August. Pupae were most abundant during the second week of August. Male and female pupae matured along with the workers, females emerging slightly before the males. By the last of August there were young males and females and many cream-colored callow workers together with the ever-diminishing number of pupae.

Autumn.—During early September all of the pupae matured, giving rise to great numbers of callow workers. By mid-October all of the callows had taken on their mature brown color and the colonies were again in their winter condition.

Position of Repletes in the Colony.—It was at first thought that repletes would provide reserve food for the colony during the winter but studies showed constant winter foraging whenever weather permitted and colonies came through to spring with no diminishing in their percentage of repletes. After flight time in the early spring almost all above ground activity ceased abruptly. This was the time of the maturing of larvae, which must therefore have been fed by the repletes. During this time there was an ever decreasing proportion of repletes, which, however, was built up again quickly when fruit became abundant in

TABLE I. *Populations of Prenolepis imparis Say colonies*

	*Sept. 19 1940	*Sept. 20 1940	*Oct. 2 1940	*Oct. 30 1940	*Mar. 15 1941	*Mar. 22 1941	*Apr. 12 1941	*Apr. 12 1941	*May 10 1941	*June 2 1941	July 15 1941	July 16 1941	July 21 1941	Aug. 13 1941	Aug. 19 1941	Aug. 19 1941	Aug. 25 1941	Sept. 6 1941	Sept. 11 1941	*Sept. 15 1941
Nest queen	2		1	1	1	1	1	1	1	1	1	1	1	1	1		1	2	1	
Workers																				
Non-repletes	378	205	384	491	202	523	130	20	323	131	50	65	107	97	333	533	208	32	143	397
Repletes	1313	1609	1824	1365	788	1720	756	28	1782	1498	21	137	320	294	395	283	175	278	261	674
Callows															64	235	388	807	892	855
Winged forms																				
Males	271	235	83		13	471											102	18	9	299
Females	22	30	45		7	41										10	10	5	26	15
Pupae																				
Worker													88	320	592	1186	260	351	32	294
Male															162	94	7	1		16
Female													15			2				
Larvae											272	377	1020	1	17	5				
Eggs											2	6								
Total	1986	2079	2337	9857	1011	2756	887	49	2106	1632	346	586	1551	723	1564	2348	1151	1496	1364	2550

Starred nests dug at St. Charles, Missouri. Unstarred nests dug at Tiffin, Ohio.
Flight of the overwintered males and females occurred April 6, 9, and 10, 1941.

Table II. *Percentage of replete workers in colonies of Prenolepis imparis during different seasons of the year*[2]

September, October, November (7 colonies)	repletes made up 78.29% of the workers.
March, April, May (5 colonies)	repletes made up 80.89% of the workers.
June, July, August (8 colonies)	repletes made up 67.20% of the workers.

[2] In this report callows were not counted, since it could not be determined whether they would mature into repletes or non-repletes.

August and September and non-repletes were actively foraging.

Nest Structure

Nest structures of animals are always of interest as an expression of the animals' physiological activity Nest structures of social insects are of particular interest in population studies because they express the activities, not of isolated individuals, but of the more significant unit of population, the colony. *Prenolepis* nests were found to be definite, rather standardized, and thoroughly characteristic of the species. For this study 20 nests were dug, but only the 11 at St. Charles, Missouri, are reported here (figures 1 and 2). The Tiffin, Ohio, nests were similar, differing only in that they were not so deep (perhaps because of the close proximity of the Sandusky River) and were not in such smooth solid clay.

Method of Digging the Nest.—First a hole 30 inches in diameter and 40 inches deep was hired dug to the side of the nest. This was large enough so that the writer could get into the hole and attack the nest from the side. Then this hole was extended to the two sides of the nest area, within 5 inches of the nest opening, leaving a column of earth containing the nest exposed on three sides. After this the actual digging of the nest began, a process which required from 3 to 5 hours. First a shelf was formed 4 to 6 inches down by cutting into the column of clay in front of the nest, then chambers and galleries were carefully excavated down to this level. The shelf was helpful because the disturbed ants fell upon it and so were easily picked up before they crawled away. As soon as the section thus exposed was drawn to scale on squared paper and all the ants were collected, another shelf was made further down and the process was repeated to the bottom of the nest. White ink was found an invaluable aid in tracing the gallery. It was squirted into the nest entrance and as digging progressed more ink was used so that there was never any doubt in distinguishing the nest gallery from other small holes which might be present in the clay.

Structure of Nest.—All of the 11 nests dug in Becker's orchard were located in solid, hard-packed, yellow clay. At the surface of the ground the nest entrance was simply a little round hole one-quarter inch in diameter. Around this there might be a fairly conspicuous ring of excavated yellow clay pellets or the entrance might be so thoroughly concealed in the grass as to make its discovery impossible except by watching ants enter and leave. Usually nest entrances were conspicuous during the time of fall activity, less so in winter, very conspicuous in the spring just before flight, and then almost obliterated during the summer lull.

Beneath the surface the gallery was usually a single central shaft which extended almost straight down and, with the chambers radiating out from it, formed a nest radius of from 2 to 5 inches. Chambers sloped up in such a way that they never became flooded with the white ink which was poured down to trace the gallery. This means that they were also protected from flooding by rains. Chambers were dome shaped and the floors, walls, and ceiling were very smooth and even. They varied slightly in size and shape but the average was 1.5 inches by 2 inches and 0.5 inch high. The first chamber occurred within an inch or two beneath the soil surface and was used as an antechamber for ants entering or leav-

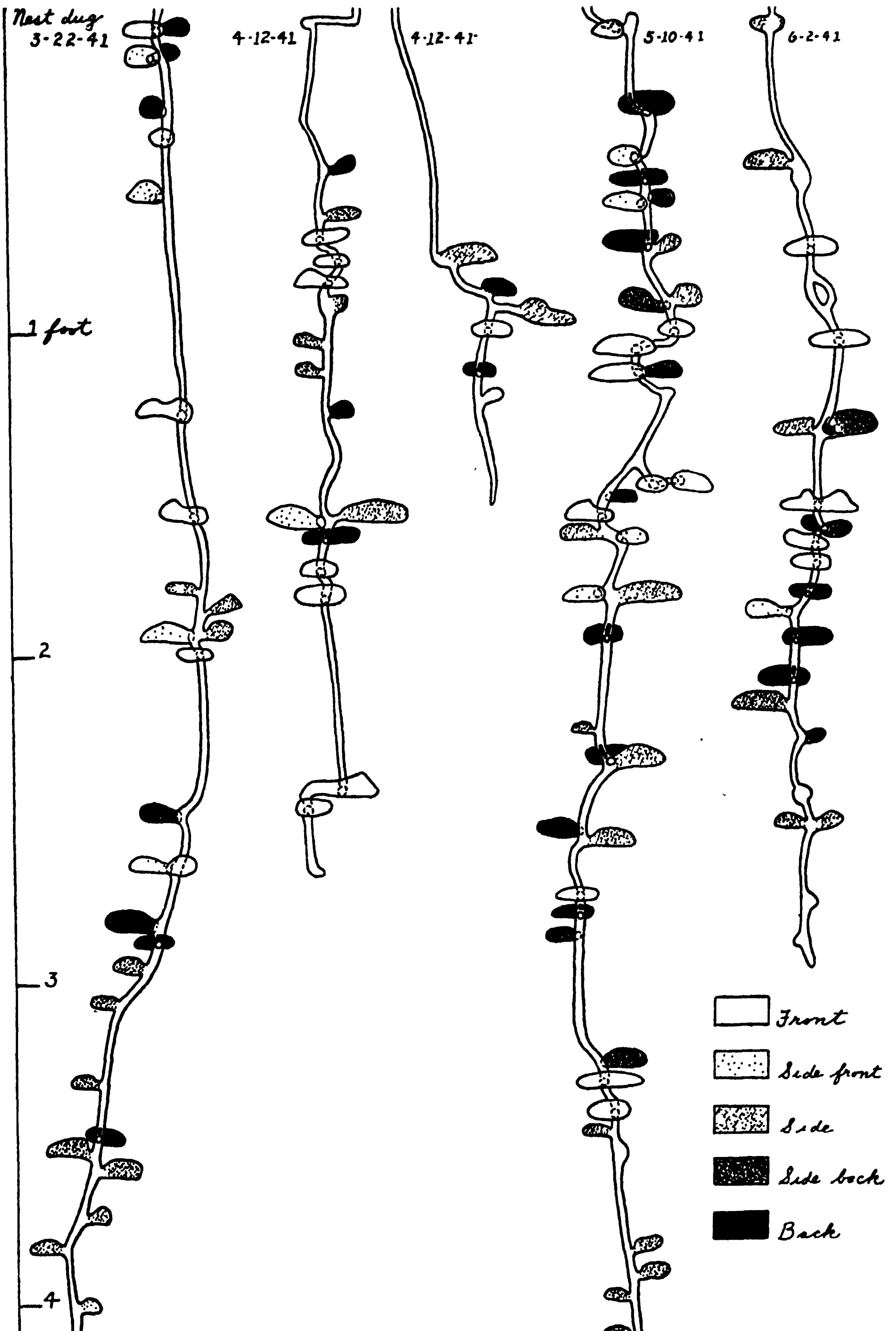

FIG. 1. *Prenolepis imparis* Say nests dug at St. Charles, Missouri.

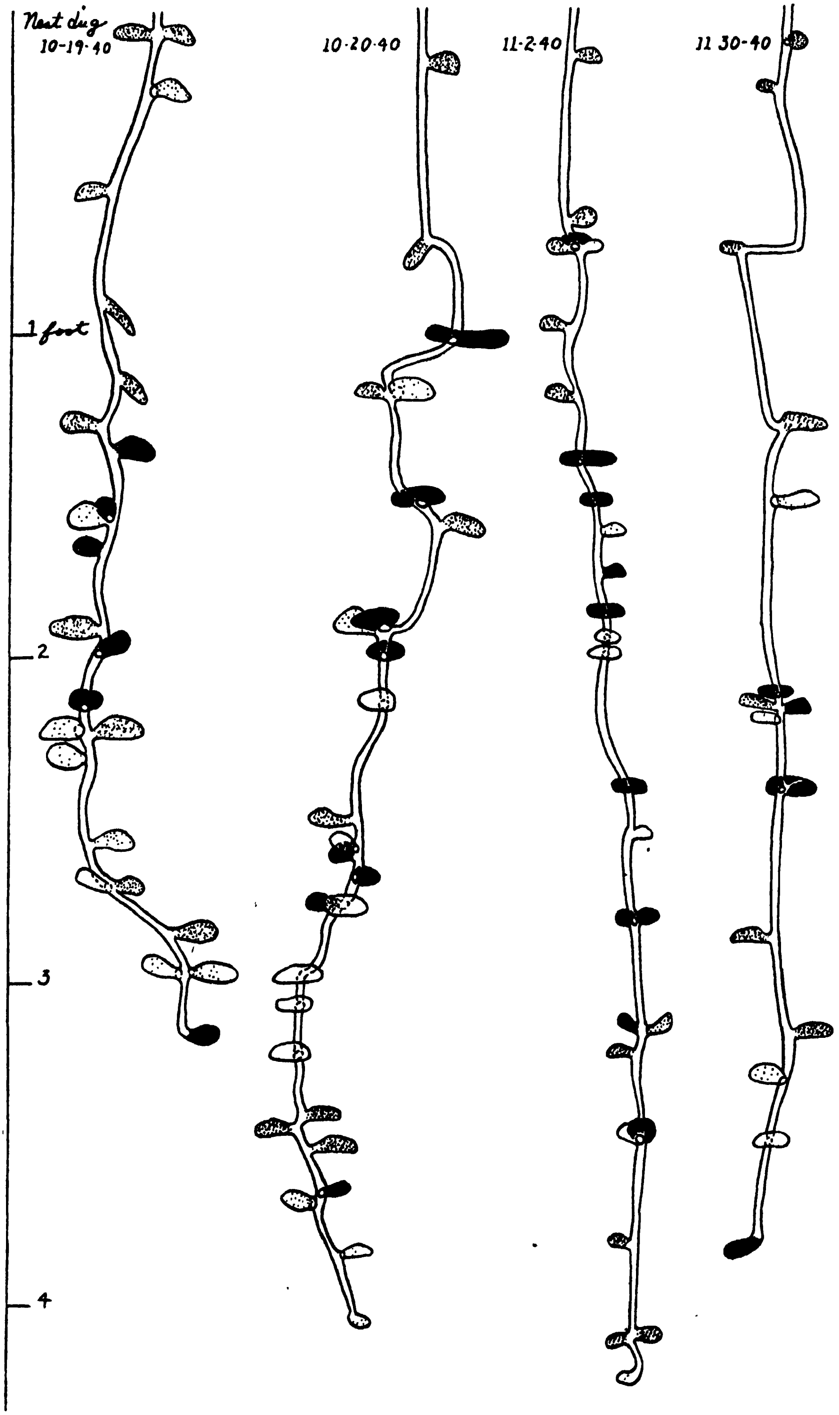

FIG. 2. *Prenolepis imparis* Say nests dug at St. Charles, Missouri.

ing the nest. Just before flight time in the spring this antechamber was enlarged into a little cluster of cells which served as a loitering place for males and females as they made short preliminary excursions into the light. The next chamber was from 4 to 8 inches below the surface and from then on chambers extended out at irregular intervals, sometimes clustered at one level and sometimes with a stretch of 6 or 7 inches between them. Nests reached various depths, but 50 or 51 inches seemed to be the limit for a mature colony.

Relation of Ants to the Nest.—Chambers varied greatly in the number of individuals they contained. Usually only non-replete workers were found in the surface chambers, but in the lower half of the nest repletes were numerous and often packed into the chambers. There was no indication that hibernating conditions made any difference in the distribution of ants in the nest. This correlates with the observation that workers foraged all during the winter whenever the temperature was above freezing. Neither did winter nests extend deeper than those in summer. The nest queen had no common location in the various nests but was more often found in the lower half. Brood was usually scattered through most of the chambers. Males and females kept well toward the depths except just before flight, when they congregated in the surface chambers. As the accompanying chart shows, there is some correlation between the size of the colony and the size of the nest.

POPULATION OF AN AREA

Ant colonies may be studied as units with a view to determining the number of such units which a given area will support. An attempt at this type of determination was made for *Prenolepis* in the Becker orchard.

TABLE III. *Comparison of the size of the Prenolepis imparis nests at St. Charles, Mo. with the size of the colony as judged by number of workers*

Date of nest digging	Depth of nest in inches	Workers per nest	Number of chambers	Average no. of workers per chamber
4-12-41	18	48	6	8.00
3-15-41	26	990	13	76.15
4-12-41	32	886	16	55.38
6-2-41	35	1629	19	85.74
10-19-40	38	1691	24	70.46
11-30-40	46	1856	15	123.73
10-21-40	49	1814	26	69.74
9-15-41	50	1926	19	101.37
3-22-41	50	2243	28	80.11
5-10-41	51	2105	39	53.97
11-2-40	51	2208	25	88.32
Average	40.54	1581.45	20.90	73.90

Counting the number of nests in an area is not possible at all times because nest openings are usually inconspicuous and are sometimes completely concealed. But in the early spring, when preparation for flight begins, there are little yellow circles of newly excavated clay about the entrances and at this time workers and the winged forms are often above ground. Accordingly, during this period of activity (beginning 3–23–41) nests were hunted and were staked as found. Then on one day of the flight period (4–9–41) all the nests so marked were plotted on squared paper to show their relationship to each other and to the fruit trees of the orchard. Eighty-eight *Prenolepis* nests was found to be the total for the orchard of 1860 square yards (figure 3). This is probably a slight undercount, since even under the most favorable circumstances some nests must have been overlooked.

Nests were not distributed uniformly over the area but were aggregated in certain places, leaving other parts almost void of colonies. Curiosity was aroused as to the factors which determined this unequal distribution. Differences in substratum could be eliminated as a determining factor since the whole orchard was located on the hard clay which was eminently suited for *Prenolepis* nest construction. The nearness of another *Prenolepis* colony probably had some influence, since nests were usually at least 4 to 8 feet from one another, although there

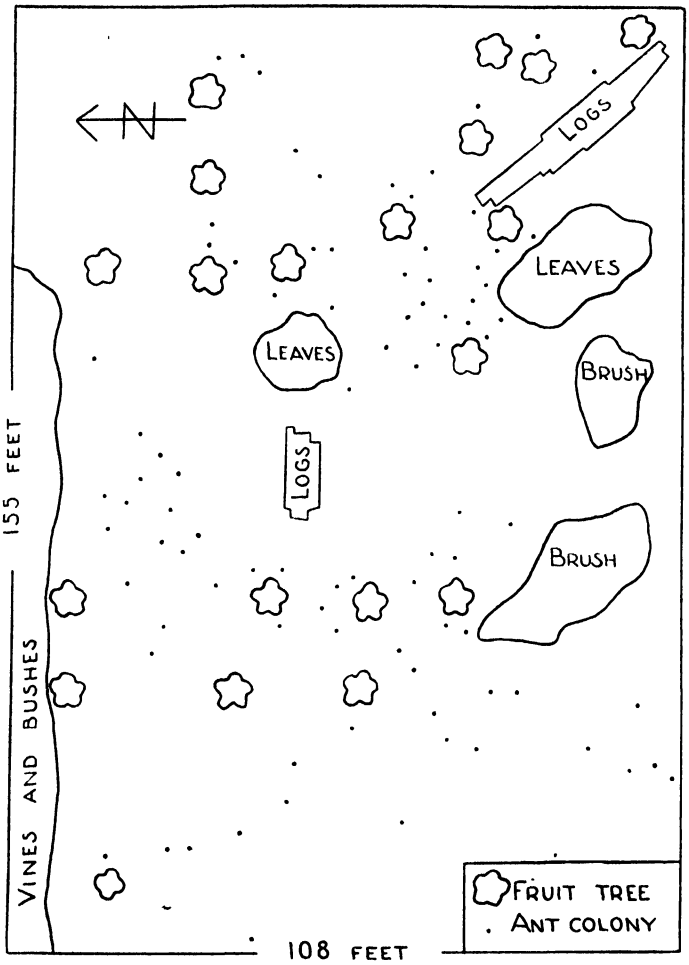

FIG. 3. Distribution of 88 *Prenolepis imparis* Say nests in an orchard at St. Charles, Missouri.

were many exceptions to this where nests were 1, 2, or 3 feet from one another, and one incipient colony was 1.5 inches from a larger nest. Nests were obviously grouped near to the large apple or other fruit-bearing trees whose decaying fruits served as the main food in the fall, and absence of such trees undoubtedly accounted for absence of nests from some parts of the orchard. But almost no colonies were found in the north-east corner, although several large apple trees were there. This lack seemed to be due to the presence in this corner of a luxuriant growth of long matted grass which formed a layer over the soil surface. *Prenolepis* colonies seemingly could not endure such a covering. Bare soil or cut grass with light shade of trees through part of the day appeared to offer the most favorable nest location.

Of course, the initial nest location is due to the activity of the female in digging below the surface and excavating a cell there. That such a location could be anything but fortuitous seems doubtful in view of the fact that on flight days great numbers of females were creeping under every shelter and down every crevice with apparently no selection whatsoever. The number of females available this year for founding colonies in the orchard was estimated as follows. About 9 out of 10 nests produced males and females because of the 7 nests dug during the fall and winter 6 contained males and females and of 11 watched during flight 10 provided winged forms. Thus it may be assumed that about 80 nests of the 88 in the orchard contained males and females. The 6 nests counted which contained winged forms showed an average of 633 males and 27 females per nest. Thus 80 nests could produce 49,540 males and 2160 females. Since females, being heavy, did not fly far, most of them remained in the orchard. Certainly only a few could have survived, perhaps because of some inherent weakness in the females or because of their many predators at this precarious period of their existence. Another explanation might be that most of the females happened to establish themselves in unfavorable places. The environmental limiting factors at this time must be those affecting the soil at the surface and to a depth of several inches. Thus a matting of heavy grass might keep the soil moist enough to encourage mold which kills females. Lafleur ('41) reports that in artificial nests young *Prenolepis* queens often fail to take necessary sanitary precautions to prevent mold from killing their young and themselves.

This initial weeding out of females is not the only way in which environmental factors can keep a population reduced. Mature colonies may be destroyed by environmental changes such as a piling up of leaves over the nest entrance, or by excavation. However, adverse local conditions do not necessarily mean the extermination of a colony, since *Prenolepis* colonies have been observed in the process of moving (Wheeler, '30). There is no evidence that mature colonies are destroyed to any appreciable extent in a well-established orchard.

Since nothing is known concerning the natural life span of a colony, there can be no estimation of the length of time that a particular area is dominated by one nest. There is, in fact, nothing to indicate that the orchard has ever reached maximum density of *Prenolepis*. The queens and young colonies may be weeded out so rigorously that there never has become a competition for food between mature colonies. This speculation as to how many colonies the orchard might be able to support leads to the question of how much ground it takes to support each colony and how much fighting is carried on to maintain this living space.

Colony Territory

Does each colony of *Prenolepis* have a distinct foraging ground? Is it maintained as a stable area or is it shifted from time to time? Are territories of nearby nests distinct or do they overlap? And finally are these areas maintained by hostilities between colonies?

To initiate this study the wanderings of individual ants had to be watched closely. It was soon found that *Prenolepis* had two distinct types of foraging activity which will be designated as (1) exploring and (2) trailing. During exploratory activities foraging individuals left the nest singly and seemed to wander at random, going back and forth, climbing up and down grass blades and touching all parts of the soil with which they came into contact. This resulted in a rather thorough patrolling of the ground, the carrying into the nest of all food which was small enough to be transported and the discovery of large pieces of food. The second type of activity—trailing—resulted after a large piece of food (decaying fruit, dead earthworm, etc.) had been found. Then a distinct odor trail was set up which individuals followed slavishly as compared to the seemingly haphazard wandering of exploring ants. Workers often left the nest in little groups of 4 to 10 and followed one after another along the invisible trail, touching antennae with those coming from the opposite direction. It was clearly evident that there was an odor trail because the ants did not necessarily travel close together and an individual a yard or more from any fellow would follow the exact trail, always going over certain grass blades or around certain pebbles, often making wholly unnecessary turns simply because the trail had been laid down that way.

The advantage for this study in choosing an ant which makes an oder trail is quite obvious. Trails were definite and their ending could be determined without confusion. Also this eliminated the need for marking individual ants in order to be sure that they actually came from a certain nest, for when a trail had been traced back to a nest there could be no doubt that the ants on it belonged to that nest. The technique for plotting such trails was simple. Brightly dyed tooth picks were placed wherever ants were seen. If the ants were merely exploring this soon showed up as a little forest of picks, scattered more or less at random. But if a trail had been found then the picks took on a linear arrangement and it was seen that the line of tooth picks was followed by subsequent ants as if they were guide posts of a highway, since the picks outlined the invisible trail.

After the habits of the ants were determined the next step was to mark all of the trails made by a series of colonies over a period of time to see if they outlined definite foraging territories. This work had to be done at Tiffin because of the time required, so an area surrounding a pear tree in the Talbot yard was selected and for a period of 44 days, from July 10 to August 31, all new trails were staked, measured, and recorded each morning. Tooth picks outlining the trails were maintained during the entire period so that new trails would not be confused with old ones. During this time pears which dropped from the tree were augmented with apples so that there would be an abundance of food.

Because of the peculiarity of *Prenolepis* in observing an almost entire cessation of above-ground activity from the flight period in the spring until midsummer or later, records of individual colonies had to begin whenever members of that colony first appeared (table IV). The individual variation shown by the colonies in ceasing the aestivation was extreme, extending as it did over a period of six weeks. Cool wet weather encouraged foraging, and hot dry weather discouraged it, but this could not be the determining factor in the "waking up" process because of the variation shown among nests in this respect. Neither could the state of maturity of the brood have caused the urge to ascend to the surface because colonies showed a remarkable uniformity in stages of development of brood.

The colonies also displayed great individuality in the amount of foraging they did. Never at any time were all nests represented above ground, no matter how favorable the weather. Darkness and rain did not retard foraging. Usually a trail was maintained to a pear or apple for several days until it became hard and dry, the number of ants on it becoming fewer and fewer, but sometimes, for no known reason, a piece of fruit was abandoned completely while still in the juicy, half rotted stage which is usually most attractive to the ants. Often exploration off the trail resulted in a branching of the trail to new fruit.

Table IV shows the time during which each trail existed and figure 4 displays the position of each nest and trail and the total number of trails for a period of 44 days. Little circles represent fruits to which the trails led. It seems quite obvious that no colony had a piece of ground which it maintained as its own over a period of time. It will be noticed that ants of one colony often traveled quite near to another nest entrance to get a piece of fruit on its other side. However, though specific areas of ground were not "private property," bits of fruit were. Never did the 2 to 50 ants which gathered on a pear belong to more than one nest. This could be shown amusingly by shaking the fruit and thereby causing the ants to run

TABLE IV. *A record of the odor trails maintained by 15 Prenolepis imparis colonies at Tiffin, Ohio, from July 19 to August 31, 1941.* Letters A to O indicate the 15 nests and each number refers to an odor trail which is plotted on figure 4. Figure 4 also shows the direction and length of each trail.

1941	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
7-19	1, 2	8	12												
7-20	1, 2	8	12												
7-21	1, 2	8													
7-22	1, 2														
7-23	1														
7-24															
7-25															
7-26															
7-28															
7-29	1, 2	8		15											
7-30	1, 2			15											
7-31				15											
8-1				15											
8-2				15											
8-3	3														
8-4	3														
8-5															
8-6															
8-7															
8-8															
8-9															
8-10	4														
8-11	2, 4														
8-12	2	9	13												
8-13	2	9	13		19, 20	23									
8-14	2, 5	9			19	23									
8-15		9	13	16	19	23, 24									
8-16	6		13	16	19	23, 24, 25									
8-17	6	10	13		19	25									
8-18	6			17	19	23	27								
8-19				17	19	23	27								
8-20				17, 18	19	23	27	31							
8-21		11		18	19	23	28		33						
8-22	6	11		17	19	23	28								
8-23	7	11	13	17	19	23	28								
8-24	6, 7	11	14	17	19	23	28			35					
8-25	7	11	14	17	19	26	28			35					
8-26	7		14				28, 29			35	37				
8-27	7	11					28					38			
8-28	7				21	26	28, 29		34	35, 36		38, 39	40	43	
8-29	7				21	26	29, 30					38, 39	40	43	
8-30		11	14		21, 22		30	32					41, 42	43	44
8-31			14		21, 22			32					41, 42		

off down the trail for home (this technique was used repeatedly in marking trails). Although figure 4 shows several pieces of fruit to have been visited by ants of more than one nest it will be noted from the dates on table IV that these visitations were not at the same time; one colony would abandon a fruit and then another would find it. The one exception to this occurred when nests E and M found a pear at the same time and put on the only definite show of hostility seen (except for very rare individual combats the ants explored and trailed with no sign of antagonism). The pear had dropped in the late morning and at noon there was discovered a large group of ants extending from each of the two nests to it. More ants were out than had ever been seen at one place before and almost the entire non-replete population (no repletes were present) of the two colonies must have been involved. All of the ants were milling back and forth along the trails touching antennae or trying to grasp each other with mandibles. Occasionally two

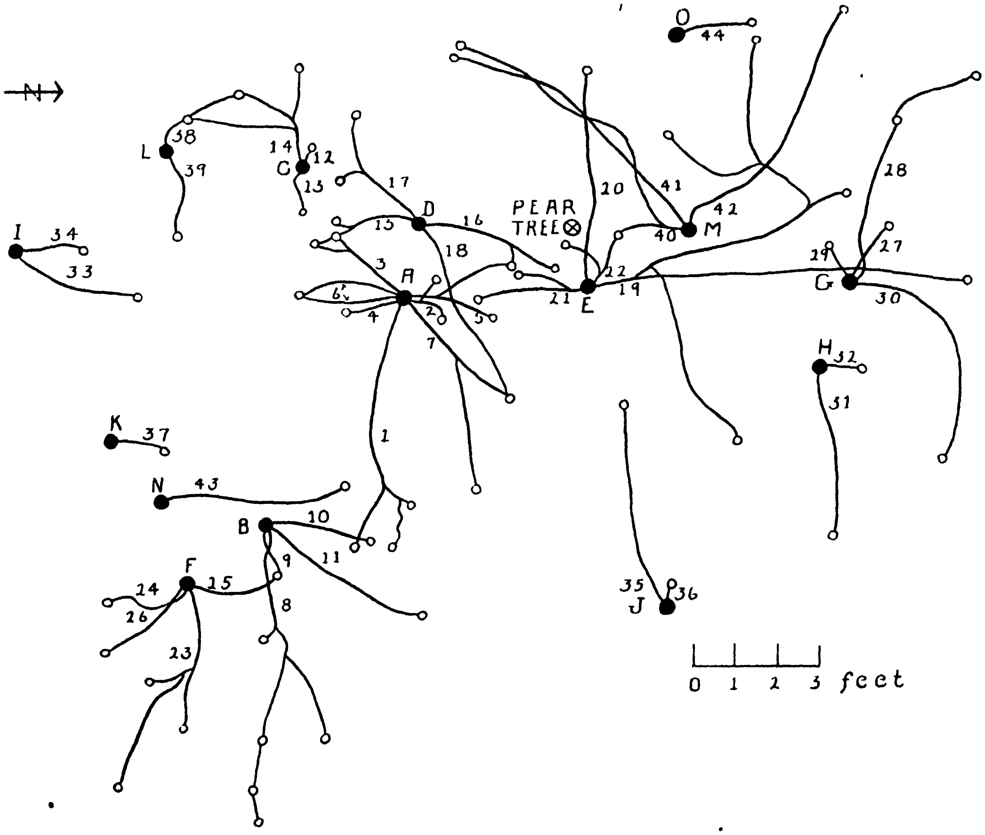

FIG. 4. Fifteen *Prenolepis imparis* Say colonies (*A–O*) grouped about a pear tree at Tiffin, Ohio, together with all of the odor trails laid down by them from July 19 to August 31, 1941. Black circles represent colonies, light circles pieces of fruit or other food; lines represent odor trails. Trail numbers correspond to those on table IV which indicate the date or dates when each trail was maintained.

rolled over and over and sometimes one dragged another along the trail for several inches before it let go and each walked away. All of this time most of the ants were simply milling up and down the trail and the whole fight was slow-motion, mild, and uneventful. Almost none got hurt; in fact, by the end of the fight only two were injured and no dead ants were seen. The largest group might from time to time be nearer one nest or the other (surprisingly only two or three were ever on the pear), but the odds of battle could never be ascertained because there was no way of telling ants of nest E from those of nest M. (At any time it took close observation to see that there was any hostility at all since only a small portion of the ants present were fighting at any time. The rest were just moving back and forth between the two nests.)

At 2:30 P.M. it was noticed that some ants from nest M were leaving the battle trail and were swinging off to the west. This deflection was more apparent at 6:45 but still there were enough individuals fighting to make the outcome of the battle problematical. By 7:45 it was certain that nest E had won the pear: twenty ants were on it eating and a steady stream extended to the nest. Nest M had abandoned its trail entirely and was actively trailing off to the west to another pear.

No battles were seen between *Preno-*

lepis and the *Lasius niger* ssp. *alienus* var. *americanus* Emery and the *Myrmica schencki* ssp. *emeryana* Fortel which were present on the same ground, although when *Prenolepis* were eating a pear they did not allow *Lasius, Myrmica,* or even wasps on it, but drove them off by the hostile tapping of antennae which invariably routed the invaders. Otherwise there seemed to be little or no inter-species competition, for pears were the main *Prenolepis* food, whereas *Lasius* and *Myrmica* subsisted mainly on small insects picked up on the ground.

Thus it would seem that individual pieces of food were claimed by colonies but patrolling ground was common to all. However there was a distinct limit to the distance away from their nests which ants would travel. The longest distance observed from any nest was trail 10 of nest E, which ended at a pear 2.89 yards away. (The distance of the fruit from the nests was always recorded, not the actual distance of the trail, since trails were often crooked and longer than necessary.) A record was kept of the length of all trails and their branches but only the longest for each nest is recorded here. They were: A—2.33 yards, B—2.33, C—1.00, D—2.25, E—2.89, F—1.60, G—1.86, H—1.39, I—1.05, J—1.67, K—0.39, L—0.72, M—2.33, N—1.47, and O—0.58 yards. The average maximum distance traveled, for the 15 colonies, was 1.59 yards.

Pickles ('35, '36, '37, '38, '40), working on the problem of territory for three species of ants in England, used the longest distance which any ants would travel from its nest as the radius of a circle, the area of which he considered to be the foraging territory of the colony. Then he calculated the "lowest density" and "economic density" of the whole area under study, lowest density being the total population divided by the census area, thus giving the number of ants per square yard for the whole field, and economic density being the total population divided by the actual foraging territories of the colonies, thus giving the ants per square yard for those parts of the field where they actually traveled.

When this same method of tabulation was tried for *Prenolepis* the following results were obtained. It was considered fairer to use the average maximum distance for the 15 colonies (1.59 yds.) rather than the maximum distance of the farthest foraging colony (2.89 yards of nest E). Using 1.59 yards as the radius of a circle, the average foraging territory for a colony is πr^2 or 7.94 square yards and for 15 colonies is 119.10 square yards. The total population of the 15 nests is calculated as 18548.25 (9 nests dug gave an average population of 1236.55). The economic density then may be figured as the total population divided by the total foraging areas and this gives 155.73 ants per square yard. In calculating lowest density the total population is divided by 56 square yards (the total area of the plot under consideration) and gives 331.22 ants per square yard. This gives a lowest density (331.22 ants per square yard) which is over twice as great as the economic density (155.73 ants per square yard) and indicates in another way the great degree of overlapping of territories which is shown on figure 4. Or can it really be called territory in this case where any particular foot of ground may be traversed by trails of as many as 3 colonies during 6 weeks of foraging?

Similar calculations for the St. Charles orchard show results as follows. It is assumed that the average maximum foraging distance worked out for Tiffin can be used for St. Charles. Thus, if 1.59 yards is the average maximum foraging distance, then the foraging area for the 88 colonies of the orchard will be 698.72 square yards. The calculated total population of 88 nests is 153984.16. The economic density then will be 220.38 ants per square yard; the lowest density is 82.78 ants per square yard, which indicates that there are large spaces of the orchard where no ant travels. It will be noticed that in this more sparse population this method of calculating gives no indication as to whether territories are huddled together and overlap or whether they are spread out with no overlapping. However, it does show that large areas of the orchard are not populated. If it is assumed that half the orchard is suitable for colonization (this seems a conservative estimation) then the lowest density will still be only 165.56 ants per square yard, which is well below the economic density. This seems to indicate that the orchard has not reached the maximum population which it is capable of supporting.

SUMMARY

1. Twenty nests of the ant *Prenolepis imparis* Say were dug during the year 1940–41 to determine nest structure, colony size, proportion of repletes to non-repletes at various times of the year, and time of maturing of brood. It was found that colonies averaged 1518.95 members; that repletes made up 78 per cent to 80 per cent of the workers during winter and spring but dropped to 67 per cent during the summer when larvae were being fed (and workers were not foraging); that brood matured at an almost even rate, eggs being laid by the middle of July; larvae pupated by the middle of August and almost all pupae emerged by mid-September. No brood was over-wintered, but males and females were retained in the nest through the winter and flew on the first warm days of spring (April 6, 9, and 10 for 1941).

2. A census of an orchard of 1860 square yards showed 88 colonies. They were most numerous near the fruit bearing trees in cut lawn and were scarce or absent where trees were lacking or where there was a heavy matting of uncut grass. Another area of 56 square yards contained 15 colonies which were centered about a pear tree and were in cut lawn. Daily records were kept of all of the trails (invisible odor trails) to pieces of fruit which were laid down by these 15 colonies for a period of 44 days. It was found that exploring ants were capable of finding food as far as 2.89 yards from the nest and made trails in all directions from the nest, but that no colony maintained a territory of ground which it defended against invasion from other colonies and that each piece of ground might be crossed by ants of several different colonies. However, bits of fruit were strictly "private property" for a colony and were defended with fighting if necessary. In the plot of 56 square yards each of the 15 colonies had a theoretical 3.73 square yards of ground (and an actually foraged 7.94 square yards, because foraging territories overlapped considerably). In the orchard of 1860 square yards each of the 88 nests had a theoretical 21.13 square yards of ground. Thus it would seem that the orchard has not reached its maximum population of *Prenolepis* (even in the portion that is undoubtedly suitable for colonization).

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THE STATISTICAL ANALYSIS OF CHAPARRAL AND OTHER PLANT COMMUNITIES BY MEANS OF TRANSECT SAMPLES

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In many field investigations some method of sampling vegetation must be employed to procure data from which can be made computations of the abundance and importance of species. The method should be both accurate and easy to use. The methods generally used in the past have been lacking in one or the other of these characteristics.

The easiest and least accurate method of ascertaining the relative importance of the several species in a plant community is by ocular estimation, which is merely making the best guess possible. The quantitative relations among the species are sometimes expressed by assigning them to abundance classes described by such terms as: very rare, rare, infrequent, locally frequent, scarce, sparse, occasional, scattered, common, copious, locally abundant, moderately abundant, abundant, moderately dense, dense and dominant. When these terms are not standardized, the assigning of species to such classes is highly subjective and the method often lacks the exactness necessary for scientific analysis. There are various methods of determining the quantitative relations among the species of a community. Most of these are based on the examination of samples, located either at random or along definite lines through the area studied. The measurements of the vegetation in these samples are tabulated and abundance or other desired matters are calculated. The methods of sampling vegetation and of presenting the results have constituted serious problems ever since Pound and Clements ('98) proposed the quadrat as an accurate means of determining the abundance of species in plant associations.

There are several distinctly different concepts in quantitative relations. These are:

(1) Numerical abundance, in which all the specimens are counted, but the individual plants are not measured in any way. The importance of a given species may be expressed as its percentage of all individuals of all the species recorded; that is, "percentage of vegetation."

(2) Frequency index or percentage, a study of distribution in which the presence of the species is noted, but individual plants are neither measured nor counted. The importance of a given species is expressed as the percentage of samples in which it occurs, taken on the area investigated.

(3) Coverage extent, in which the area of ground covered by the crown, or other portion, of each individual plant is measured. The importance of a given species is assumed to be expressed by either the per cent of the total ground surface that it covers or as its percentage area in the total area covered by vegetation recorded.

(4) Volumes for each species.

(5) Dry weight and per cent of total dry weight for each species produced per unit of time.

Review of the Literature

Methods of making statistical analyses of vegetation have been discussed extensively and ably by a number of ecologists. A great deal of the discussion has centered around Raunkiaer's ('09, '18) frequency

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[1] The writer wishes to acknowledge his indebtedness to Dr. Paul G. Hoel, Department of Mathematics, University of California at Los Angeles, for help with the mathematical aspects of the paper. Officials of the San Dimas Experimental Forest, particularly Mr. Jerome S. Horton, provided certain data and rendered numerous other favors. In making both the laboratory and the field tests much help was given by Robert Erdman, Horace Haskell, Harold Lint, Harry Thompson and David Osborn.

method, and attempts by various investigators to calculate abundance from formulae and other theoretical devices. The size, shape, and location of the sample plots have also received attention.

Among the early contributions to the subject were those of Arrhenius ('21, '22, '23) and Gleason ('20, '22, '25). Kenoyer ('27), in his study of Raunkiaer's work, included an excellent summary of the statistical methods used up to that year. Hanson and Ball ('28) applied the frequency method to grazing studies. Gleason ('29) showed that frequency percentages vary considerably with the size of the quadrat employed. Nichols ('30) emphasized the importance of quadrat and coverage data. Romell ('30) cautioned against comparing statistics based on different-sized sample plots and pointed out the advantage of areal or coverage measurements over frequency. Hanson and Love ('30) compared and discussed the merits of five methods of quadratting. Christidis ('31) recommended that sample plots be as long and narrow as possible to reduce the effect of heterogeneity.

In an extensive discussion of sociological concepts Cain ('32) commented on the terminology used in analyzing and describing vegetation and pointed out the error of considering species of high frequency as necessarily being dominant. Hanson ('34) compared several methods of analyzing the native prairie of North Dakota. McGinnies ('34) discussed both the theoretical aspects and field applications of quadrat sampling and frequency calculations in several types of vegetation in Arizona.

Blackman ('35) recommended the "percentage of absence" of species as a means of studying changes in density. Ashby ('35) criticized much of the work in statistical ecology as being based on unsatisfactory assumptions, such as that of complete random distribution in plant communities. Singh and Das ('39) studied the relation between frequency percentages and density in weed flora. Pechanec and Stewart ('40), in an investigation of the sagebrush range of Idaho, found that long narrow sample plots were generally somewhat more efficient than square ones of the same size, and concluded that in selecting sampling devices a balance must be struck between sampling accuracy and such practical considerations as the time and effort required.

Although numerous investigations involving quantitative analysis of vegetation have been carried out in herbaceous and forest communities, very few studies have been reported for scrub or brush communities. Nelson ('30) described a method of charting shrubby vegetation for planimeter measurements. Adamson ('31), in studying the brush cover of South Africa, found that samples located at random gave about the same results as those located in straight lines. Horton ('41) made statistical analyses of the Californian chaparral and concluded that the milacre plot is a suitable size sample for bringing out important ecological relationships in this type of vegetation, but calls attention to the great amount of time required to complete the field and office work.

Until recently practically no reports of quantitative analyses of vegetation based on transect sampling rather than on quadrats, have appeared in the literature. Bauer ('36, pp. 422–426), in an investigation of the Californian chaparral, gave a brief account of transect sampling in which the distance that each individual plant spread over the line was recorded and used as the basis for various calculations. Hasel ('41), in a study of reproduction in forests, used a method of linear measurement as a substitute for mapping. Canfield ('41) described the line interception method as applied to range studies.

Since transect sampling has been used so seldom in the past, it is apparent that the workers either assume that transect data are not valid or that they have overlooked its advantages. The writer (Bauer, '36), in attempting to make a quadrat study of the brush cover of the Santa Monica Mountains, encountered so many difficulties that he was forced to conclude that extensive quadratting in a dense thicket was impractical. As a result, the transect method was adopted and much more satisfactory results were obtained.

Although small two-dimensional sample plots can be located quickly in herbaceous vegetation by dropping a wire or iron frame on the ground, this is not true of vegetation made up largely of shrubs or trees. In scrub and forest communities a transect can be run and the desired data recorded in a small fraction of the time required to establish a quadrat and make corresponding records. This is especially true if direct measurements of the individual plants are to be made as a means of determining ground coverage from which the relative importance of the species can be computed. However, questions may be raised as to the representativeness and accuracy of transect data as compared with quadrat data. The chief purpose of this paper is to compare the efficiency of the transect and the quadrat methods of sampling vegetation, and also to compare several different methods of expressing a given set of measurements.

LABORATORY TESTS

In order to get information as to the relative accuracy of the transect and quadrat methods of sampling, and also as a means of comparing the accuracy of several methods of expressing data, a series of laboratory tests was carried out. In these, cardboard discs of various colors were spread out on a specially prepared board or table top of one square meter, in such a way as to simulate a plant community. Each color represented a species and each disc an individual plant. The discs were cut to definite sizes and the number used was such that the area covered and the percentage of the whole was known for each color. The sizes and proportions were intended to approximate roughly those found in the Californian chaparral.

Before the samples were taken the discs were thoroughly mixed and spread on the board by hand. No conscious effort was made to place any particular disc or color in any particular place. An attempt was made to distribute the discs over the surface with fair uniformity, by avoiding pile-ups and noticeably large bare spaces. The total area covered by all the discs was in every case the same as that of the board, namely 10,000 square centimeters. Since the discs were circular, there was some overlapping and there were some interstices among them. Each disc within the sample area was recorded completely, even though it might be partly covered by another disc. The bare spaces were not recorded.

After the discs were scattered over the board, the assemblage ("community") was sampled by means of four transects and four quadrats. The samples were located at random, but one transect and one quadrat were taken somewhere near each corner of the board. The transects were taken along the edge of a transparent 30 cm. celluloid ruler. The distance that each sampled disc extended along the transect line was measured and entered on a specially prepared form.

The quadrat samples were taken by means of a square (10 cm. on each side) marked on a transparent piece of celluloid. The area of each disc, or portion of a disc, inside the quadrat was recorded. In order to get complete coverage, all pieces were recorded, even though the center of the disc was outside the square. Where only a portion of the disc was inside the quadrat, its area was measured by matching with previously prepared pieces of known size.

After the eight samples (four transects and four quadrats) were posted, the discs were picked up, thoroughly mixed, and redistributed over the board. Two hundred assemblages ("communities") were sampled in each of the four tests made.

Test 1

In the first test all the discs were of the same size, each having an area of ten square centimeters. One hundred discs of each color were used, and each of the ten colors, therefore, constituted ten per cent of the entire assemblage.

Table I shows the results of the measurements made in the first test. The figures given are percentages of all the discs ("vegetation") recorded for each of the three concepts. "Coverage" is the complete coverage of the line or in the quadrat, being based on measurements of each individual disc. In the "numerical abundance" part of the table, the number of discs of each color was used as a basis for the percentage calculations, rather than the measurements of the individual discs.

TABLE I. *Percentages of colors ("species") in 200 assemblages ("communities") composed of dissc ("plants") which were all of the same size and in which each color was equally abundant*

Color	Actual per cent of all colors ("Vegetation")	Data based on measurements by the transect method		Data based on measurements by the quadrat method	
		Per cent as measured	Deviation	Per cent as measured	Deviation
Data based on coverage measurements					
Black	10.00	10.43	0.43	9.57	0.43
Brown	10.00	9.91	0.09	9.65	0.35
Blue	10.00	10.20	0.20	10.39	0.39
Violet	10.00	9.34	0.66	9.89	0.11
Indigo	10.00	9.92	0.08	10.15	0.15
Green	10.00	9.98	0.02	9.91	0.09
Yellow	10.00	9.67	0.33	10.24	0.24
Orange	10.00	10.42	0.42	9.94	0.06
Red	10.00	10.45	0.45	10.20	0.20
White	10.00	9.75	0.25	10.00	0.00
Average			0.293		0.202
Data based on numerical abundance					
Black	10.00	10.56	0.56	9.44	0.56
Brown	10.00	9.81	0.19	9.65	0.35
Blue	10.00	10.24	0.24	10.34	0.34
Violet	10.00	9.16	0.84	10.04	0.04
Indigo	10.00	10.08	0.08	10.37	0.37
Green	10.00	9.80	0.20	9.93	0.07
Yellow	10.00	9.86	0.14	10.10	0.10
Orange	10.00	10.46	0.46	9.79	0.21
Red	10.00	10.34	0.34	10.40	0.40
White	10.00	9.77	0.23	9.93	0.07
Average			0.328		0.251
Data based on frequency					
Black	10.00	10.44	0.44	10.07	0.07
Brown	10.00	10.18	0.18	9.92	0.08
Blue	10.00	10.02	0.02	9.94	0.06
Violet	10.00	9.55	0.45	9.79	0.21
Indigo	10.00	9.76	0.24	10.07	0.07
Green	10.00	9.91	0.09	9.95	0.05
Yellow	10.00	9.63	0.37	10.01	0.01
Orange	10.00	10.32	0.32	9.94	0.06
Red	10.00	10.27	0.27	10.25	0.25
White	10.00	9.88	0.12	10.01	0.01
Average			0.255		0.087

In the "frequency" part of the table, neither measurement nor counting of the individuals was used. The percentages given are based on the frequency of occurrence of a given color in all the samples taken. In tabulating frequency, several discs of a certain color are not weighted any more heavily than a single one of the same color that touches some part of the 30 cm. transect or is found inside the 10 cm. quadrat.

The most noticeable thing about table I is the close agreement between the two methods of sampling and also between the three methods of expressing the results. The percentages based on quadrat samples, especially where based on frequency, are slightly more accurate than those based on transect samples. In the case of coverage, the average amount of deviation of the composition percentages as measured, from the actual percentages is 0.29 for the transects and 0.20 for the quadrats.

The slightly better showing of the quadrats is probably due to the fact that the set-up favored the quadrats. The transect used was rather short, being only three times longer than the side of the quadrat. In order to be equivalent, two sampling devices should yield about the same number of statistical items. In this test the quadrats included about 38 per cent more items than did the transects. It should also be remembered that in a natural community of mixed species not all of the plants will have the same size body, and the species will not be of equal abundance.

Test 2

In the second test the procedure was the same as in the first except that the colors were not equally abundant. The black and the brown each constituted 25 per cent of the entire assemblage, but the red and the white only 1.5 per cent. The total surface covered by the ten colors was the same as in the first test. The purpose was to find out which method of sampling would give better results in the case of the colors ("species") present in small percentages.

Data for the second test are given in table II. The average amount of deviation under the conditions of this test is considerably greater than in the first test, but there is still no appreciable difference between the transect and the quadrat methods of taking the samples. Based on coverage, the average amount of deviation for the transects is 1.006 and that for the quadrats is 0.983. When the percentages are based on numerical abundance the results are practically the same as when coverage is used.

Since all the discs used in this test were of the same size, the percentages in the samples should be directly proportional to the numbers used, and the mathematical expectancy would be, therefore, the same as the percentage composition of the entire assemblage ("community"), in the case of coverage and numerical abundance. In the case of frequency, however, this is not true because of the element of probability. The mathematical expectancies were calculated from the following formulae:[2]

$$\text{for the transects, } F = 1 - (1 - P)^N$$

$$\text{for the quadrats, } F = 1 - (1 - P')^N.$$

In these formulae, "F" is the frequency expected, "N" is the number of discs of a given color used, "P" is the probability of a disc being included in a transect sample, and "P'" is the probability of a disc being included in a quadrat sample. The probability is calculated from the formulae,

$$\text{for the transects, } P = \frac{2ar + \pi r^2}{A^2}$$

$$\text{for the quadrats, } P' = \frac{b^2 + 4br + \pi r^2}{A^2} .$$

In these formulae, "a" is the length of the transect line, "r" is the radius of the

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[2] The formulae used for calculating the mathematical expectancies were provided by Dr. Paul G. Hoel, Assistant Professor of Mathematics, University of California at Los Angeles.

TABLE II. *Percentages of colors ("species") in 200 assemblages composed of discs of uniform size but in which the colors were of different abundance*

Color	Number of discs	Actual per cent of all colors ("Vegetation")	Data based on measurements by the transect method			Data based on measurements by the quadrat method		
			Mathematical expectancy	Per cent as measured	Deviation	Mathematical expectancy	Per cent as measured	Deviation
Data based on coverage measurements								
Black	250	25.00	25.00	22.61	2.39	25.00	22.34	2.66
Brown	250	25.00	25.00	22.34	2.66	25.00	22.99	2.01
Blue	125	12.50	12.50	13.50	1.00	12.50	12.94	0.44
Violet	125	12.50	12.50	12.82	0.32	12.50	12.26	0.24
Indigo	75	7.50	7.50	8.60	1.10	7.50	8.44	0.94
Green	75	7.50	7.50	7.97	0.47	7.50	8.21	0.71
Yellow	35	3.50	3.50	3.93	0.43	3.50	4.19	0.69
Orange	35	3.50	3.50	3.69	0.19	3.50	3.93	0.43
Red	15	1.50	1.50	2.52	1.02	1.50	2.45	0.95
White	15	1.50	1.50	1.98	0.48	1.50	2.26	0.76
Average					1.006			0.983
Data based on numerical abundance								
Black	250	25.00	25.00	22.83	2.17	25.00	22.69	2.31
Brown	250	25.00	25.00	22.28	2.72	25.00	23.23	1.77
Blue	125	12.50	12.50	13.20	0.70	12.00	12.79	0.29
Violet	125	12.50	12.50	12.86	0.36	12.50	12.00	0.50
Indigo	75	7.50	7.50	8.70	1.20	7.50	8.36	0.86
Green	75	7.50	7.50	7.98	0.48	7.50	8.23	0.73
Yellow	35	3.50	3.50	5.97	0.47	3.50	4.22	0.72
Orange	35	3.50	3.50	3.65	0.15	3.50	3.96	0.46
Red	15	1.50	1.50	2.42	0.92	1.50	2.29	0.79
White	15	1.50	1.50	2.10	0.60	1.50	2.27	0.77
Average					0.977			0.920
Data based on frequency								
Black	250	25.00	16.89	16.59	0.30	14.78	15.08	0.30
Brown	250	25.00	16.89	16.33	0.56	14.78	14.98	0.20
Blue	125	12.50	13.74	13.55	0.19	13.42	13.42	0.00
Violet	125	12.50	13.74	13.11	0.63	13.42	12.35	1.07
Indigo	75	7.50	10.46	10.63	0.17	11.15	10.80	0.35
Green	75	7.50	10.46	10.14	0.32	11.15	10.84	0.31
Yellow	35	3.50	6.02	6.18	0.16	7.06	7.11	0.05
Orange	35	3.50	6.02	5.48	0.54	7.06	6.62	0.44
Red	15	1.50	2.89	4.17	1.28	3.58	4.35	0.77
White	15	1.50	2.89	3.57	0.68	3.58	4.39	0.81
Average					0.483			0.430

disc used, "b" is the side of the quadrat and "A" is the side of the square area over which the entire assemblage is distributed.

The formula for the quadrats is similar to the one used by Gleason ('20) for calculating the frequency index. The formula used here, however, recognizes the fact that the effective quadrat used had rounded corners. Since all discs within the quadrat were recorded, even though their centers were outside, the effective size of quadrat actually used was 10 cm. plus the diameter of the disc, as shown in figure 1.

The formula for computing the mathe-

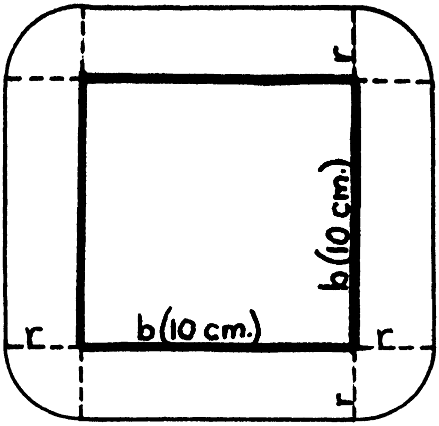

FIG. 1. Diagram showing the shape and other details of the effective quadrat used in sampling simulated plant communities, and from which the probabilities were calculated. Formulae and explanations in the text.

matical expectancies in the case of the transect is based on the fact that the probability of a certain disc touching the transect line is the same as the probability of the center of that disc falling within an area as long as the line, having a width of one diameter, and having a half disc added at each end. Such an area is illustrated in figure 2.

When the percentages based on frequency data are compared with the mathematical expectancies calculated according to the formulae given, a remarkable agreement is noted in the case of both the transect and the quadrat sampling, the average deviations being 0.483 and 0.430 respectively.

In the case of both methods of sampling and of each method of expressing the results, the percentages calculated from the measurements are somewhat too low for the colors constituting high percentages of the whole, and somewhat too high for the colors constituting low percentages of the whole.

Test 3

In the third test the discs were not all of the same size, but the area covered by each color was the same, namely 1,000 sq. cm., and each color, therefore, constituted 10 per cent of the total surface covered. The assemblage consisted of 10 black and 10 brown discs, each having an area of 100 sq. cm.; 13⅓ blue and 13⅓ violet discs, each having an area of 75 sq. cm.; 20 indigo and 20 green discs, each having an area of 50 sq. cm.; 40 yellow and 40 orange discs, each having an area of 25 sq. cm.; and 100 red and 100 white discs, each having an area of 10 sq. cm. The purpose of this test was to see if either of the two sampling devices had greater efficiency than the other in sampling colors ("species") which consisted of a comparatively few large individuals rather than of numerous small ones. This arrangement, of course, resembles a natural community of mixed species more closely than was the case in either of the previous tests.

Data for the third test are given in table III. The mathematical expectancies in the case of coverage data is the same as the percentage composition of the entire assemblage. The expectancies for the frequency data were calculated from the formulae given on page forty-nine. For the numerical abundance data, the expectancies for the transect samples were calculated from the formula *NP*, and those for the quadrat samples from the

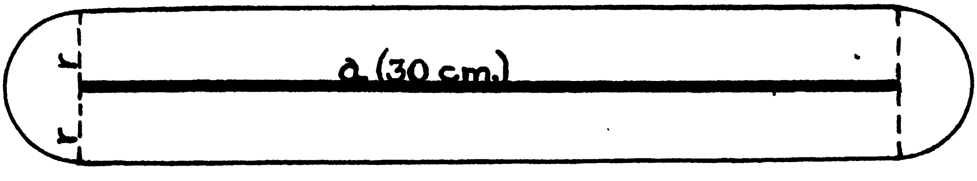

FIG. 2. Diagram showing the shape and other details of the area used in calculating the probability of a disc touching the transect used in sampling assemblages of colored discs. Formulae and explanations in the text.

TABLE III. *Percentages of colors ("species") in 200 assemblages composed of discs ("plants") of various sizes but in which each color covered the same area*

Color	Actual per cent of all colors ("Vegetation")	Data based on measurements by the transect method			Data based on measurements by the quadrat method		
		Mathematical expectancy	Per cent as measured	Deviation	Mathematical expectancy	Per cent as measured	Deviation
Data based on coverage measurements							
Black	10.00	10.00	11.48	1.48	10.00	8.05	1.95
Brown	10.00	10.00	10.61	0.61	10.00	8.80	1.20
Blue	10.00	10.00	8.63	1.37	10.00	8.08	1.92
Violet	10.00	10.00	9.90	0.10	10.00	9.88	0.12
Indigo	10.00	10.00	10.50	0.50	10.00	8.86	1.14
Green	10.00	10.00	9.51	0.49	10.00	9.47	0.53
Yellow	10.00	10.00	9.10	0.90	10.00	11.86	1.86
Orange	10.00	10.00	10.15	0.15	10.00	11.31	1.31
Red	10.00	10.00	9.90	0.10	10.00	12.00	2.00
White	10.00	10.00	10.09	0.09	10.00	11.65	1.65
Average				0.579			1.368
Data based on numerical abundance							
Black	10.00	6.35	7.23	0.88	4.94	4.69	0.25
Brown	10.00	6.35	6.75	0.40	4.94	4.95	0.01
Blue	10.00	7.10	6.50	0.60	5.73	4.62	1.11
Violet	10.00	7.10	7.17	0.07	5.73	5.63	0.10
Indigo	10.00	8.38	8.32	0.06	7.20	6.65	0.55
Green	10.00	8.38	7.90	0.48	7.20	6.95	0.25
Yellow	10.00	11.25	10.93	0.32	11.06	11.00	0.06
Orange	10.00	11.25	11.54	0.29	11.06	11.50	0.44
Red	10.00	16.93	16.54	0.39	21.07	21.58	0.51
White	10.00	16.93	17.08	0.15	21.07	22.48	1.41
Average				0.364			0.469
Data based on frequency							
Black	10.00	7.43	8.45	1.02	6.60	6.28	0.32
Brown	10.00	7.43	7.89	0.46	6.60	6.77	0.17
Blue	10.00	8.07	7.25	0.82	7.38	6.23	1.15
Violet	10.00	8.07	8.31	0.24	7.38	7.48	0.10
Indigo	10.00	9.13	9.60	0.47	8.72	8.20	0.52
Green	10.00	9.13	8.83	0.30	8.72	8.45	0.27
Yellow	10.00	11.16	10.59	0.57	11.57	11.99	0.42
Orange	10.00	11.16	11.29	0.13	11.57	12.06	0.49
Red	10.00	14.21	13.87	0.34	15.70	16.47	0.77
White	10.00	14.21	13.86	0.35	15.70	16.00	0.30
Average				0.470			0.451

formula *NP'*. In these formulae, "*N*" is the number of circles used, "*P*" is the probability for the transects and "*P'*" the probability for the quadrats, these probabilities being calculated from the formulae previously given.

Inspection of the table shows that when data are based on frequency, the two sampling devices are about equally accurate, but when coverage or numerical abundance was used the transects were more accurate than the quadrats. The advantage is especially marked in the case of the coverage data, the average deviation for the transects being 0.579 and that for the quadrats 1.368. As sampled by transects and expressed as coverage, the percentages show about the same deviation for all colors. However, as sampled by quadrats, there is a marked tendency for the percentages of those colors present as a few large discs to be too low and for those of the colors present as numerous small discs to be too high. This may be due to the fact that the transect has greater linear extent and reaches into more of the entire area being sampled.

Test 4

In the fourth test the colors varied as to the amount of surface covered, and each color consisted of three different-sized discs. There was also variation among the colors as to the average size of the three discs. Details of the composition of this assemblage are given in table IV. The plan was to simulate as nearly as possible the conditions in a natural community of mixed species. In such a community the species not only vary as to the amount of ground surface covered but also as to the characteristic sizes of the plants.

Results of the fourth test are given in table V. The mathematical expectancies for the coverage data are the same as the percentage composition of the entire assemblage. The expectancies for the numerical abundance data were computed from the following formulae:

for the transects, $N_1P_1 + N_2P_2 + N_3P_3$

for the quadrats, $N_1P'_1 + N_2P'_2 + N_3P'_3$.

The expectancies for the frequency data were computed from the following formulae:

for the transects, $F = 1 - (1 - P_1)^{N_1} \times (1 - P_2)^{N_2} \times (1 - P_3)^{N_3}$

for the quadrats, $F = 1 - (1 - P'_1)^{N_1} \times (1 - P'_2)^{N_2} \times (1 - P'_3)^{N_3}$.

In the above formulae the subscripts refer to each of the three sizes of discs of which each color is composed in this test. The symbols are the same as in the formulae previously given.

TABLE IV. *Numbers and areas of discs used in Test IV, and the percentages of total surface covered*

Color	Number of discs used	Area of disc. Sq. cm.	Area covered	Percentage of total coverage
Black	10 10 10	100 80 60	1000 800 600	24
Brown	10 10 10	100 80 60	1000 800 600	24
Blue	7 6 7	80 60 40	560 360 280	12
Violet	7 6 7	80 60 40	560 360 280	12
Indigo	7 6 7	60 40 20	420 240 140	8
Green	7 6 7	60 40 20	420 240 140	8
Yellow	6 5 6	40 20 10	240 100 60	4
Orange	6 5 6	40 20 10	240 100 60	4
Red	6 5 6	20 10 5	120 50 30	2
White	6 5 6	20 10 5	120 50 30	2

Examination of table V shows that the results of the fourth test are about the same in principle as those obtained in the third test. Transect and quadrat sampling are about equally accurate when the percentages are based on frequency and on numerical abundance. However, the transect has a distinct advantage when coverage data are considered, the average deviation being 0.719 for the transect and 1.181 for the quadrat. The tendency of both methods to give percentages too low for the more abundant colors and too high for the less abundant one is apparent.

In tables I, II, III and V, the data,

TABLE V. *Percentages of colors ("species") in 200 assemblages of discs ("plants") in which the colors varied as to the amount of surface covered, and in which each color consisted of discs of three different sizes*

Color	Actual per cent of all colors ("Vegetation")	Data based on measurements made by the transect method			Data based on measurements made by the quadrat method		
		Mathematical expectancy	Per cent as measured	Deviation	Mathematical expectancy	Per cent as measured	Deviation
Data based on coverage measurements							
Black	24.00	24.00	22.61	1.39	24.00	21.09	2.91
Brown	24.00	24.00	22.31	1.69	24.00	21.56	2.44
Blue	12.00	12.00	12.12	0.12	12.00	12.41	0.41
Violet	12.00	12.00	11.48	0.52	12.00	11.44	0.56
Indigo	8.00	8.00	9.14	1.14	8.00	8.94	0.94
Green	8.00	8.00	8.47	0.47	8.00	9.39	1.39
Yellow	4.00	4.00	4.33	0.33	4.00	5.23	1.23
Orange	4.00	4.00	4.63	0.63	4.00	4.94	0.94
Red	2.00	2.00	2.37	0.37	2.00	2.55	0.55
White	2.00	2.00	2.53	0.53	2.00	2.44	0.44
Average				0.719			1.181
Data based on numerical abundance							
Black	24.00	20.44	18.90	1.54	18.59	16.95	1.64
Brown	24.00	20.44	18.78	1.66	18.59	17.52	1.07
Blue	12.00	11.42	11.41	0.01	10.84	10.76	0.08
Violet	12.00	11.42	11.03	0.39	10.84	10.01	0.83
Indigo	8.00	8.90	9.92	1.02	9.09	9.64	0.55
Green	8.00	8.90	9.49	0.59	9.09	9.50	0.41
Yellow	4.00	5.50	5.70	0.20	6.33	7.27	0.94
Orange	4.00	5.50	6.01	0.51	6.33	6.63	0.30
Red	2.00	3.75	4.11	0.36	5.15	6.08	0.93
White	2.00	3.75	4.65	0.90	5.15	5.65	0.50
Average				0.718			0.725
Data based on frequency							
Black	24.00	17.04	16.68	0.36	15.56	15.18	0.38
Brown	24.00	17.04	16.23	0.81	15.56	15.20	0.36
Blue	12.00	11.82	11.73	0.09	11.13	11.46	0.33
Violet	12.00	11.82	11.39	0.43	11.13	10.58	0.55
Indigo	8.00	9.80	10.12	0.32	9.78	9.75	0.03
Green	8.00	9.80	10.51	0.71	9.78	9.75	0.03
Yellow	4.00	6.62	6.55	0.07	7.35	7.83	0.48
Orange	4.00	6.62	6.75	0.13	7.35	7.22	0.13
Red	2.00	4.71	4.84	0.13	6.18	6.69	0.51
White	2.00	4.71	5.20	0.49	6.18	6.32	0.14
Average				0.354			0.294

regardless of whether the measurements were recorded as numerical abundance, frequency or coverage, were given as "per cent of vegetation," in order to make valid comparisons. In the case of coverage measurements, the data might better be presented as the actual area covered. If the two-dimensional quadrats truly represent the entire community, the percentage of coverage within the quadrats is also the percentage of coverage in the larger area. In the case of the transect, however, it might be questioned whether or not the percentage of the sample line cov-

TABLE VI. *Relation of the percentage of the line covered in the transect samples and the percentage of the surface area covered in the quadrat samples to the true percentage of coverage in the large assemblage ("community")*

Color	True per cent of coverage in larger assemblage	Transect sampling		Quadrat sampling	
		Per cent of line covered	Deviation	Per cent of area covered	Deviation
Discs of uniform size; colors equally abundant					
Black	10.00	10.76	0.76	9.74	0.26
Brown	10.00	10.22	0.22	9.82	0.18
Blue	10.00	10.52	0.52	10.57	0.57
Violet	10.00	9.64	0.36	10.07	0.07
Indigo	10.00	10.23	0.23	10.34	0.34
Green	10.00	10.30	0.30	10.09	0.09
Yellow	10.00	9.97	0.03	10.43	0.43
Orange	10.00	10.75	0.75	10.12	0.12
Red	10.00	10.78	0.78	10.39	0.39
White	10.00	9.95	0.05	10.17	0.17
Average			0.40		0.26
Discs of uniform size; colors not equally abundant					
Black	25.00	19.89	5.11	19.43	5.57
Brown	25.00	19.66	5.34	19.98	5.02
Blue	12.50	11.88	0.62	11.25	1.25
Violet	12.50	11.28	1.22	10.64	1.86
Indigo	7.50	7.56	0.06	7.32	0.18
Green	7.50	7.01	0.49	7.14	0.36
Yellow	3.50	3.46	0.04	3.64	0.14
Orange	3.50	3.24	0.26	3.41	0.09
Red	1.50	2.22	0.72	2.13	0.63
White	1.50	1.74	0.24	1.96	0.46
Average			1.41		1.55
Discs of various sizes; each color covering same area					
Black	10.00	11.43	1.43	7.82	2.18
Brown	10.00	10.57	0.57	8.55	1.45
Blue	10.00	8.59	1.41	7.85	2.15
Violet	10.00	9.87	0.13	9.60	0.40
Indigo	10.00	10.42	0.42	8.67	1.33
Green	10.00	9.47	0.53	9.19	0.81
Yellow	10.00	9.10	0.90	11.52	1.52
Orange	10.00	10.12	0.12	10.99	0.99
Red	10.00	9.86	0.14	11.65	1.65
White	10.00	10.10	0.10	11.31	1.31
Average			0.57		1.37
Discs of various sizes; colors varying as to area covered					
Black	24.00	23.66	0.34	21.08	2.92
Brown	24.00	23.34	0.66	21.55	2.45
Blue	12.00	12.68	0.68	12.40	0.40
Violet	12.00	12.00	0.00	11.43	0.57
Indigo	8.00	9.56	1.56	8.94	0.94
Green	8.00	8.86	0.86	9.38	1.38
Yellow	4.00	4.52	0.52	5.23	1.23
Orange	4.00	4.84	0.84	4.94	0.94
Red	2.00	2.48	0.48	2.55	0.55
White	2.00	2.65	0.65	2.44	0.44
Average			0.659		1.182

ered is also the percentage of the surface area covered in the larger area.

Table VI is a comparison of the true percentage of the surface covered by the colored discs with the percentage of the line covered in the case of the transects and the percentage of the area covered in the case of the quadrats. It is apparent that the transect samples and the quadrat samples indicate the actual percentage of coverage with about equal accuracy in the case of those assemblages composed of individuals of uniform size (a situation rarely found in natural vegetation). It is rather surprising to note that in the assemblages composed of individuals of various sizes (the usual condition in natural plant communities) the transects indicate coverage in the larger area with considerably more accuracy than quadrats. In the assemblage that most nearly resembles a natural community, the average deviation for the transects was 0.659 and that for the quadrats 1.182.

FIELD TEST

The information derived from the laboratory tests on simulated plant communities, described in the preceding pages, may have some practical applications in field studies involving the determination of the composition of the vegetation or other characteristics of plant communities. The transect method of sampling appears to have some definite advantages over quadrat sampling in certain types of vegetation, such as scrub or forest, where the individual plants are large enough and sufficiently well-defined to be measured quickly and accurately. Data based on transects, which involve measuring the plants in one dimension only, can be obtained in a small fraction of the time required to establish and make chart quadrats. Moreover, when coverage of the ground is considered or is taken as a basis for calculating percentage composition, data based on transect sampling appear to be more accurate, especially in mixed communities where individuals vary considerably as to size.

In order to test the transect method of sampling vegetation under field conditions, it was tried out on certain plots in the San Dimas Experimental Forest of the California Forest and Range Experiment Station, located near Glendora, California. At this forest, extensive studies of the relations between chaparral vegetation and moisture conditions are being made. The experimental work being done here is described by Kraebel and Sinclair ('40). The area used to make the test was a set of nine "Run-off and Erosion Plots" located on a northeasterly exposure with a slope of about 20 to 25 per cent. The chaparral vegetation here is tall and the stand so dense that much of it can be traversed only on hands and knees. Each plot is 10 ft. wide by 125 ft. long.

This area was selected because intensive quadrat studies of its floristic composition have been carried on for some years, and its percentage composition of species is probably known with more exactness than that for any other available area. In making the study the Forest Service has charted the entire surface of the nine plots graphically and to scale. Almost annually since 1935 this area has been carefully and completely measured. To do this requires, for each charting, about twenty man-days or 160 hours of time. Observations of herbage and litter are made as well as observations on the shrubby cover.

In measuring this area by the transect sample method, a single thirty-meter transect was run through each of the nine plots. A steel tape was used. The extent of crown projection along the line from either above or below, was measured and recorded in a specially prepared form. The sampling device used simulated a vertical plane transect rather than a line transect.

A summary of the data obtained by the two methods is given in Table VII. The figures given are percentages of composition, and are based on coverage measurements. There is fair agreement between the four-year averages of the two methods of measuring. The percentages of most

TABLE VII. *Percentage composition of species in the vegetation of nine run-off plots of the San Dimas Experimental Forest. Percentages are based on coverage*

Plant species	Measurements made in				4 year average
	1936	1938	1939	1941	
Data obtained from forest service quadrats					
Adenostoma fasciculatum	0.52	0.84	0.74	0.81	0.73
Arctostaphylos glauca	1.28	1.18	0.93	0.99	1.09
Ceanothus crassifolius	25.46	26.08	21.24	21.46	23.61
Ceanothus oliganthus	10.00	10.03	10.89	10.88	10.44
Cercocarpus betuloides	12.58	12.76	14.27	14.37	13.45
Photinia arbutifolia	2.22	2.37	2.80	3.38	2.67
Prunus ilicifolia	0.74	1.17	1.38	0.89	1.06
Quercus dumosa	46.58	45.16	47.30	46.70	46.51
Rhamnus crocea var. *ilicifolia*	0.34	0.27	0.38	0.32	0.33
Rhus ovata	—	0.01	0.04	0.14	0.03
Data obtained from transect samples					
Adenostoma fasciculatum	0.74	0.52	1.06	0.65	0.76
Arctostaphylos glauca	2.82	4.43	2.43	1.00	2.65
Ceanothus crassifolius	23.62	24.86	23.81	20.85	24.03
Ceanothus oliganthus	12.40	9.63	8.00	7.10	9.34
Cercocarpus betuloides	9.96	9.39	7.80	18.97	11.32
Photinia arbutifolia	2.20	2.11	2.85	2.98	2.58
Prunus ilicifolia	0.74	1.19	0.98	1.00	1.04
Quercus dumosa	43.14	46.85	52.28	46.64	47.48
Rhamnus crocea var. *ilicifolia*	0.82	—	—	0.71	0.20
Rhus ovata	0.96	0.36	0.72	0.14	0.56

of the species are surprisingly alike. In the case of *Arctostaphylos glauca* and *Cercocarpus betuloides* (all plant names according to Jepson, '25) the difference is more noticeable, but still the percentages are close enough to have considerable value.

In view of the short time required to take the transect samples, the similarity in the results of the two methods of measuring is remarkable. Only about three man-hours were required for the transects, whereas about 160 man-hours were spent in quadratting the area. It is probable that a few more hours spent in taking additional transects would yield practically the same results as charting the entire ground surface. It should be noted that in this field test, transect samples are not being compared with quadrat *samples* but with a 100 per cent charting of the entire area. Such complete charting is an accurate method but is not practical on a large area. It can only be used on small areas and when plenty of help is available. For most field investigations, a sampling method must be employed.

It should be remembered that the chaparral plots in which the field test was made was a particularly difficult sample of vegetation in which to work. The thicket was so dense that it could not be easily traversed, and, because of the overlapping branches, the limitations of the individual plants were often not clear. Moreover, the species were not uniformly distributed, some of them having a tendency to occur in patches in certain parts of the area. In spite of these handicaps fairly good results were obtained with a comparatively few transect samples which required only a few hours to take. With a more open type of vegetation, or a somewhat larger number of transects, still more accurate results would be expected.

Discussion

A study of the results of the laboratory tests shows that percentages based on transect sampling compare fairly well with percentages based on quadrat sampling in all cases, and that in some instances the transects gave decidedly more accurate results than the quadrats. Quadrat sampling appears to have a slight advantage in the assemblages composed of individuals of uniform size (a condition not generally found in nature) and in all cases where the percentages are based on frequency. In those assemblages composed of individuals of various sizes (the usual condition in nature) transect sampling appears to have a slight advantage when the percentages are based on numerical abundance, and a very decided advantage when they are based on coverage.

The advantages of the transect method may be even more pronounced than is indicated, in view of the fact that the experimental set-up used appears to favor the quadrat method. In order to make the fairest comparisons, the two sampling devices should yield about the same number of items. The thirty centimeter transect used did not include as many plants as the quadrat. In Tests 1 and 2, in which the assemblages consisted of discs of uniform size, about 38 per cent more entries were made in the quadrat record than in the transect record. In Tests 3 and 4, in which the discs were of various sizes including a number of comparatively large ones, over 12 per cent more items were entered in the quadrat than in the transect record. In spite of this advantage, the quadrats did not give markedly better results at any point, and in some cases, as noted above, were decidedly less accurate than the transects.

Numerical abundance data do not take into account the fact that plant bodies vary as to size. In counting, a small plant is weighted just as heavily as a large one, although it obviously produces less vegetation than a large one. This is an important matter in mixed communities where plants vary considerably in size. A species characterized by large individuals has greater importance in an association than a species composed of small plants, even though both species may have the same numerical abundance.

Frequency index data are subject to misleading interpretations, such as assuming that species of high frequency are necessarily "dominant" (Cain, '32). It has been shown (Gleason, '29) (Kenoyer, '27) that when the frequencies are grouped in the five frequency classes (A, B, C, D, & E) as is often done, the resulting ratios depend in large measure on the size of the quadrat sample used. In order to demonstrate Raunkiaer's law, different-sized sample plots must be used for different associations. For a given association quite different results are obtained when the size of the sample plot is varied. This brings into frequency index data an element of uncertainty that is undesirable in the quantitative analysis and comparison of different associations. Comparisons of vegetation cannot be made where different-sized quadrats have been used (Romell, '30). Frequency index tabulations are, however, useful to show uniformity, or lack of uniformity, in the distribution of species—that is, the degree of homogeneity of an association.

Coverage data have some distinct advantages. They provide a sound basis from which the percentage composition of the vegetation can be calculated, because they take into account the fact that plants vary as to size. In addition, coverage can be expressed as the actual amount of the ground surface covered, an important ecological character. It is coverage rather than numbers of plants or frequency of occurrence or other quantitative concepts used in the analysis of vegetation that determines dominance and gives character to a community. Because of these things coverage data may be thought of as more valuable and significant than other data intended to express the quantitative relations among species.

The time and labor involved in recording coverage data in the past have tended to discourage its extensive use. When quadrats are used as a basis for such computations, the individual plants are sometimes charted to scale and, later, the area of each measured with a planimeter (Hanson and Love, '30). Even when the areas within the quadrats are estimated instead of actually measured, much time is required and it may be doubted whether the results justify the labor.

The transect method of sampling vegetation, as described herein, offers a real saving of time and trouble in obtaining data as to coverage or other ecological relations with no loss of accuracy whatever. Indeed, the laboratory tests carried out indicate that, in mixed communities, transect sampling gave decidedly more accurate percentages of coverage than quadrat sampling. It is not clear why this is true but it is probably due to the fact that the transect has greater linear extent than the quadrat and reaches into more of the entire area being sampled.

The transect is not only suitable for obtaining data as to coverage, numerical abundance and frequency, as discussed above, but can be adapted to show other structural characteristics of vegetation. By recording appropriate units or items in the field record, it is probable that such characters as density, openness, luxuriance and volume can be ascertained with considerable accuracy. Since transects can be recorded in a small fraction of the time required to make the corresponding records from quadrats, investigators should give careful consideration to the possibilities of this method of sampling.

SUMMARY

A series of laboratory tests involving measurements of simulated plant communities of known composition was conducted for the purpose of comparing the relative efficiency of the transect and the quadrat methods of sampling vegetation for statistical analysis. Comparisons were also made between three different concepts of quantitative relations, namely, (1) coverage, (2) numerical abundance and (3) frequency, or percentage of occurrence in the samples taken.

It was found that in communities in which the individuals were all of the same size (an unnatural condition) the transect and the quadrat methods of sampling were of about equal accuracy. Transect sampling, however, has the advantage of requiring much less time. In communities in which the individuals were of various sizes (the usual situation in nature) the transects gave decidedly more accurate results when the data were based on coverage measurements. This was probably due to the greater linear extent of the transects.

Comparisons of data obtained from the laboratory tests showed that, in the case of assemblages composed of individuals of various sizes, the per cent of the line covered in the transect samples was a considerably more accurate indication of the true areal coverage in the entire assemblage than was the per cent of the area covered within the quadrat samples.

A field test of transect sampling was made in the Californian chaparral, the main watershed cover in southern California. This shrubby thicket was so dense that much of it could be traversed only on hands and knees. The results, considering the comparatively small amount of time involved, compared very favorably with the results of a chart quadrat survey which covered the entire area studied and which required a great deal of time to make.

It is probable that transect sampling deserves a much wider use than has been made of it in the past. It appears to be well suited for use in scrub or other communities where the extent of the individual plants can be clearly observed. It is likely that most of the relations that can be determined from quadrat samples can also be determined from transect samples by making the proper adaptations, without loss of accuracy but with a very considerable saving of time.

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THE EFFECT OF LOW CONCENTRATIONS OF CARBON DIOXIDE ON THE CLEAVAGE RATE IN FROG'S EGGS

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The second author and his associates have reported numerous instances in which aggregated organisms exhibit a heightened rate of metabolic activity as compared with scattered or isolated individuals (Allee, '31, '34, '38). An often made suggestion concerning the initiation of such increased activity is that it results from the somewhat higher concentration of carbon dioxide which accumulates in or near the aggregation. The presence of more carbon dioxide may well be stimulating for illuminated green plants which have a trophic use for this gas. The respiratory activities of insects and vertebrates are known to be accelerated by relatively small accumulations. The question remains, however, whether other sorts of general protoplasmic activity are regularly quickened in a similar manner.

High carbon dioxide tensions are known to be inhibitory for many processes. Other inhibiting agents are frequently stimulating in smaller concentrations. A range of carbon dioxide concentration has been demonstrated for a number of organisms below which some measurable rate of activity is decreased. As will be shown in more detail in the discussion these include, among others, the rate of growth of bacteria (Buchanan and Fulmer, '30), germination of mould spores (Durrell, '24), growth of populations of the protozoan, *Chilomonas paramecium* (Jahn, '36), *Polytomella caeca* and *Astasta longa* (Rahn, '41), the rate of division of cells in tissue culture (Mottram, '28), the growth in body length of plutei of sea urchins (Vernon, '95), the early development of the hen's egg (Romanoff and Romanoff, '33) and is suggested for the respiratory rate of Paramecium (Root, '30). However, the early rate of oxygen consumption in Arbacia eggs (Root, '30) and of early cleavage of Arbacia eggs (Smith and Clowes, '24, Haywood and Root, '30) and the early cleavage of frog's egg (this paper) is more rapid the lower the carbon dioxide tension.

MATERIALS AND METHODS

The frogs were bought from local Chicago dealers or from collectors in Michigan. Eggs were obtained by pituitary injections and fertilization was accomplished according to the directions of Rugh ('34) with some modifications which will be described shortly. Frogs were kept in the laboratory in glazed earthenware jars lined with moist paper towels at a temperature of 6° C. not only through the winter but also past the usual breeding season until the end of May. In late spring, however, the percentage of fertility decreased. At the time of pituitary injection the frogs were placed in a room held at approximately 16° C. and all further procedures were carried out there.

In our hands standard treatment called for one female or two male pituitaries per cubic centimeter of water. In the winter two injections of 2 cc. each were given. The amount required decreased in the spring until by May one injection of 0.5 cc. was usually sufficient. The females were ready to strip sooner in the spring. Eggs were used as soon as they were ready or the frog could be placed at 6° C. for a few hours. If half the eggs were stripped, the remaining unshed eggs would retain their fertilizability for a week if held at 6° C. The sperm suspension made from testes of non-injected frogs would keep at this temperature for two days at

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[1] We are indebted to Dr. Janet Wilder Dakin for access to her unpublished data on this subject and to Dr. Charlotte Haywood for reading the manuscript critically.

least and still give a high percentage of fertilization.

Eggs were stripped into a clean Petri dish or onto heavy paraffin paper. The paper was cut to fit the bottom of a Petri dish and a handle was left with which it could be manipulated. The eggs were gently apposed one, or a few at a time, to the paper to which they usually stuck, the paper did not affect the rate of cleavage. A sperm suspension of two testes in 5 cc. of water was poured over the attached eggs and the dish was gently shaken to moisten all the eggs.

Treatment following fertilization varied considerably at different times. In the first three experiments all the eggs from one female were fertilized, kept flooded with sperm suspension for 30 minutes, and a half hour later, 60 minutes after fertilization, they were cut apart and counted out in groups of 100 into liter flasks with water of different carbon dioxide tensions. In later experiments, the eggs were placed in finger bowls with water of different carbon dioxide tensions 30 minutes after fertilization and at 60 minutes they were transferred to flasks with corresponding tensions. Still later (the experiments given in table II) the eggs were separated after fertilization into small groups or gently scraped together into piles with forceps and needles; and after 20 to 30 minutes treatment with the sperm suspension, they were placed in flasks by careful handling with curved forceps. Thus one change of water and transfer of eggs were omitted and the eggs were placed in the experimental flasks a half hour after fertilization.

When paraffined paper was used, the eggs were stripped onto it one at a time, or in numbers up to ten; one or two was the usual number. These were the last 18 experiments which were performed. The results are summarized in line three of table I. The eggs were kept moist by reflooding with sperm suspension for about 20 minutes and then the paper was divided between the different experimental and control flasks. Usually there were between 50 and 150 eggs per flask; at times the numbers were purposely varied from 20, or even 10, to 100.

The eggs were killed near the middle of the second, third or fourth cleavage. In the experiments recorded in this paper, the eggs from paired and comparable experimental and control flasks were killed simultaneously by pouring them into 50 per cent formalin which thus became diluted to approximately three per cent or by placing the paper to which the eggs were attached directly into three per cent formalin. The time at which the eggs should be killed was estimated by watching cleavage in one batch of eggs at a somewhat higher temperature and then, for more accurate timing, by watching another batch of eggs which were placed under conditions exactly like the control flasks of the experiment.

The number of cleavages per 100 eggs was calculated from counts on the fixed eggs. If 100 per cent of the eggs were two-celled, the number of cleavages per 100 eggs would be 100; if half had gone through second cleavage, the number would be recorded as 150. Eggs were said to have cleaved when there was any indication of a furrow.

We have experienced difficulty in securing high percentages of fertilized eggs. None of the experiments were included in table I which had less than 50 per cent cleavage. The different series included there averaged 80 per cent cleavage.

Synthetic pond water was prepared by adding the following amounts of reagent quality chemicals to a liter of good distilled water; 50 mgm. $MgSO_4 \cdot 7H_2O$, 100 mgm. $CaCl_2 \cdot 4H_2O$, 50 mgm. $NaNO_3$ and 50 mgm. K_2SO_4. This water has been much used in experimental work in our laboratory: we used it throughout except for the sperm suspensions in certain of the early tests which were made up in Hull Laboratory well water. No difference was noted which was related to the type of water.

The distilled water contained a considerable amount of carbon dioxide. It was brought to equilibrium with the compressed air of the laboratory by aerating an almost full 20-liter carboy for at least 12 hours. This water was called normal-tension water. If a higher carbon dioxide content was wanted, an appropriate amount of water was added which was saturated with carbon dioxide. For lower than atmospheric tensions, the water was aerated with compressed air which had passed through an extended train that included NaOH followed by distilled water. The carbon dioxide tension was adjusted in a carboy from which the water was siphoned carefully into the experimental flasks. Usually no change was detected in the flasks after an eight-hour experimental period. For very low tensions, the flasks were aerated continuously throughout the experiment with air from an extended train which contained NaOH followed by distilled water on one line and distilled water alone on the other. The eggs were protected from agitation due to the bubbling.

A modification of Van Slyke's method (Oesting, '34) was used for CO_2 determination in the first 33 experiments. This measures total carbonates. Seyler's ('94) method for free carbon dioxide in the water was used in experiments 33–61 and Tashiro's ('17) method of gas analysis was used in experiments 62–80 on the air of the train. In our hands, Seyler's method was more accurate than that of Van Slyke: it showed an average deviation of 0.02 ± 0.005 * as compared with 0.10 ± 0.03 cc. per liter for the latter, and was less time consuming. Van Slyke values calculated for free carbon dioxide were 0.67 ± 0.04 cc. per liter higher than Seyler values for the same samples. Routine tests were made by one of these methods on samples from egg-containing flasks after the close of the regular experiment.

The values obtained even by Seyler's method were high when compared with calculations based on the air containing 0.03 per cent of carbon dioxide. Krogh ('41) states that in the streets of cities this value may reach 0.04 per cent. Our determinations were still higher and we cannot say whether the higher values resulted from our technique or from the actual presence of more than the normal amount of carbon dioxide in the air which we tested. Our analyses indicate that the laboratory compressed air varied from 0.045 to 0.055 per cent carbon dioxide and averaged 0.05. All three methods were used for tensions below those in atmospheric equilibrium although Tashiro's method of quantitative estimation of the carbon dioxide in the air from the train was most employed. It is difficult to compare accurately results obtained from the three methods for the small amounts of carbon dioxide. Corrected Van Slyke values ranged from -0.14 to $+0.17$ cc. per liter; the Seyler ones from 0.11 to 0.28 cc. per liter and the Tashiro tests indicated that in some experiments the air bubbled through the flasks contained less than 1.0×10^{-7} grams of carbon dioxide in 10 cc. of air. Most of the tests showed more than this amount which is equivalent to 5.5×10^{-3} cc. per liter if the same concentration is maintained as in the sample.

EXPERIMENTAL RESULTS

The data obtained are summarized in table I. Each experiment contained a number of paired flasks at or near the two carbon dioxide tensions whose effects were being compared. The results from these were all averaged together for any given experiment and then those from all similar experiments were again averaged to give the results shown in the table.

The tensions which are being compared are listed as below atmospheric, at atmospheric, or at some multiple of atmospheric equilibrium. Such equilibrium is regarded as that which we obtained by bubbling our compressed air through synthetic pond water; this was about 0.5 cc. per L. It is difficult to give exact values for the tensions we have listed as being

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* Standard error.

TABLE I. *A summary of experiments concerning the effects of different amounts of carbon dioxide (given here in terms of that present in the laboratory atmosphere) upon the rate of cleavage of frog's eggs*

Tabular line	No. expts.	Mean CO_2		Mean % cleavage retardation at higher CO_2 level	Statistical[a] probability
		Lower	Higher		
1	25	Below Atmos.	Atmos.	3.3	0.1222
2	22	Below Atmos.	Atmos.	4.5	0.0586
3	18	Below Atmos.	Atmos.	5.2	0.0420
4	20	Atmos.	1.5 × Atmos.	4.2	0.0048
5	31	Atmos.	2.1 × Atmos.	7.1	0.0008
6	12	Atmos.	3.3 × Atmos.	16.0	0.0006
7	19	1.5 × Atmos.	2.1 × Atmos.	3.4	0.38
8	8	2.1 × Atmos.	3.3 × Atmos.	2.4	0.400

[a] A statistical probability of 0.05 (approximately three times the probable error, or twice the standard error) was taken as the upper limit of statistical significance.

below atmospheric equilibrium. We have a considerable amount of evidence that in the critical experiments these usually ranged between 0.1 and 0.5 of an atmosphere.

Cleavage was retarded by the higher carbon dioxide tensions in each comparison. When these values are analyzed for their statistical probability, the first and the last two are found to lack statistical significance, while the second and third values lie just above and just below an often accepted upper limit of such significance. It is worth noting that when eggs in water at atmospheric equilibrium are compared with those from water with more carbon dioxide, there is an increase in the retardation with the higher carbon dioxide tensions and a corresponding increase in statistical significance. While larger amounts of carbon dioxide also appear to be depressing when small supra-atmospheric tensions are compared with those which are somewhat higher, differences are small and the statistical analysis shows that they are not significant.

Unpublished data collected by Dr. Janet Wilder Dakin indicate that the larger amounts of carbon dioxide are depressing when various tensions are compared ranging up to 53.3 cc. per L. These depressions usually ran about 15 per cent; in one instance, however, eggs in 40.3 cc. per L. were retarded 47 per cent as compared with accompanying eggs in 22.9 cc. per L. of carbon dioxide. The probability value in this instance was 0.01 which indicates good statistical significance.

The first three lines of the tabulated data require further explanation. Each line summarizes experiences with eggs at atmospheric as compared with those in sub-atmospheric tensions of carbon dioxide. The first line is based on all available data on this point and included those from three experiments when, as will be mentioned soon, we obtained results with an opposite trend. In the second line these early experiments are omitted and the remaining ones are summarized. In four of these 22 experiments, part of the eggs were bunched together while others were isolated. There is evidence given later that bunched eggs are less affected by differences in carbon dioxide tension than are isolated eggs; such grouped eggs may very well control the carbon-dioxide tension within their immediate environment so as to off-set the experimental differences. When these experiments also are omitted, as they are in the third line of the table, we have a summary of our most critical evidence on the relative action of sub-atmospheric as compared with atmospheric tensions of carbon dioxide. These 18 experiments were the last ones performed and were made as carefully and critically as accumulated experience allowed; results from all experiments made during this final period are included. We are strongly inclined to take seriously the indicated 5.2 per cent retardation.

The relation between percentage of retardation and the amount of carbon dioxide present is shown graphically in figure 1. Cleavage rate in water at equilibrium with the atmosphere is placed at zero retardation. This value is compared with rates shown in larger amounts of carbon dioxide to the right, and with smaller amounts to the left. The points shown are from lines 3, 4, 5 and 6 in table I. Each comparison is made between the rate of cleavage in water at equilibrium at the indicated partial pressure and that in equilibrium with the laboratory atmosphere. All these differences are statistically significant. As stated earlier, the mean amount of carbon dioxide in the sub-atmosphere tensions is not known with precision. The probable range for these experiments is indicated by the broken line. The average was probably nearer the lower than the higher part of the range, hence the point indicated by the intersection with the trend line is approximately correct. The trend line was drawn arbitrarily between zero at one atmosphere of partial pressure and the mean retardation at 3.3 times that tension.

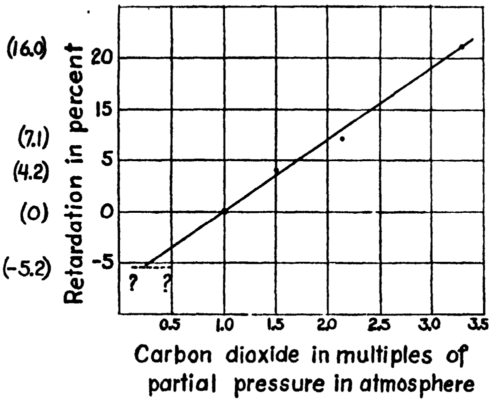

FIG. 1. The relation between carbon-dioxide tension and the percentage of retardation. Cleavage rate at one atmosphere's partial pressure is placed at zero.

With the one exception mentioned earlier, the general trend of results was similar throughout our whole series of 80 experiments which extended during the working period for two and a half years. This exception occurred during November and early December of 1939 when a series of six experiments gave opposite results, these were the first experiments performed. They included 37 paired flasks and tested all of the tension comparisons shown in table I. The mean cleavage was accelerated 6.56 per cent in the higher carbon dioxide tensions; this value has a statistical probability of 0.00003 when these six experiments are considered together; this indicates high statistical significance. Repeated efforts were made to duplicate these results without success and we have no explanation for this exception to the usual trend.

A series of 14 experiments were performed in April and May, 1940 to test the relative effects of small differences in carbon dioxide upon the rate of cleavage of frog's eggs when scattered over the bottom of the experimental flask in groups that averaged only five eggs each, as compared with others which were aggregated in one or two bunches. In all we have data from 148 flasks which are summarized in table II. It should be remembered that the data from these experiments have been incorporated in the general summary given in table I.

The experiments summarized in the first six lines of data were performed in one series of ten experiments; the number of eggs present varied from 50 to 100 per flask. In the four experiments (24 flasks) summarized in the last line, each flask contained 20 to 100 eggs, all aggregated. The mean trend is uniformly in favor of a higher rate of cleavage at the lower tensions. The differences are statistically significant only with the first comparison with isolated eggs. When all the scattered eggs mentioned above are considered together, those at the higher tension are retarded by an average of 4.7 per cent; this has a statistical probability of 0.0007 and

TABLE II. *The relation between the state of aggregation and the effect of different tensions of carbon dioxide on cleavage*

Tabular line	No. flasks	State of aggregation	Mean CO_2		Mean % retardation at higher CO_2	Statistical probability
			Lower	Higher		
1	31	Scattered	1.0 × Atmos.	1.5 × Atmos.	6.2	0.002
2	28	Scattered	1.5 × Atmos.	2.1 × Atmos.	3.3	0.145
3	18	Scattered	1.0 × Atmos.	2.1 × Atmos.	7.1	0.061
4	33	Aggregated	1.0 × Atmos.	1.5 × Atmos.	1.9	0.370
5	32	Aggregated	1.5 × Atmos.	2.1 × Atmos.	2.4	0.320
6	30	Aggregated	1.0 × Atmos.	2.1 × Atmos.	3.6	0.172
7	24	Aggregated	Below Atmos.	1.0 × Atmos.	1.7	0.550

has high statistical validity. Similarly when the aggregated eggs which were tested at the same time (lines 4, 5 and 6 in table II) are considered together, the mean retardation is 2.9 per cent with a probability of 0.1096 which is not statistically significant. When the eggs below atmospheric pressure of carbon dioxide are included with the other aggregated eggs, the mean retardation is 2.8 with an insignificant probability of .1615.

It is apparent that difference in carbon dioxide tension has more effect when the eggs are scattered. This result is not surprising. Needham ('31) cites evidence that frog's eggs retain considerable carbon dioxide from the maternal environment which is given off over a period of 100 minutes following laying. Both this carbon dioxide and that produced by respiration would diffuse more slowly from the aggregated eggs and would make these less sensitive to relatively small changes in their environment than are scattered and relatively isolated eggs.

It was not our problem to investigate the effect of aggregation as compared with isolation upon the rate of cleavage of these eggs and we have nothing to report on this interesting question.

DISCUSSION

The observation that frog's eggs will pass early cleavages more rapidly if in water with very low amounts of carbon dioxide calls to mind the early observation of Bataillon ('96) that frog's eggs would develop normally in an air stream which was saturated with water and which was said to be free from carbon dioxide. Bataillon's so-called carbon dioxide-free air probably contained about the same amount of this gas as did the air bubbled through our flasks in our better experiments at sub-atmospheric tensions.

The retarding effect of slight increases in carbon dioxide upon the early cleavages of the frog's egg invite comparisons with similar observations concerning other developing eggs. Arbacia eggs are depressed in respiration (Root '30) and cleavage by any increase in carbon dioxide. In the words of Haywood and Root ('30) "A measurable delay of cleavage occurred at tensions of carbon dioxide of as low as 4 mm. of Hg. Retardation was progressively greater up to 120–130 mm. Hg at which point complete suppression occurred." Earlier, Smith and Clowes ('24) had also reported retardation of cleavage in this egg with increased CO_2 tensions. They found that Asterias eggs were also retarded in cleavage in increased carbon dioxide tensions if put in the experimental conditions ten minutes after fertilization; if placed in heightened carbon dioxide as the eggs neared first cleavage, about 100 minutes after fertilization, they were stimulated at times for two or three cleavages. This result was not always obtained. Afterwards the stimulated eggs fell back more or less in line with the controls. After the first two cleavages eggs of Asterias were no longer sensitive to small increases in carbon dioxide.

The present analyses do not permit a decision concerning the effect of delay in placing the frog's eggs under increased carbon dioxide tension nor do they indicate whether the initial retardation would last beyond the first few cleavages.

The effect of carbon dioxide upon rate of cleavage may be related to its effect on mitosis. Mottram ('28) made counts of mitoses in tissue cultures with carbon dioxide tensions which ranged from 0 to 200 mm. Hg. Below 25 mm. and above 55 mm. the number of mitoses was lower than it was between these two values.

Bellamy ('22) reported that 0.0002 and 0.00005 normal HCl added to water which was rich in carbonates produced acceleration in the rate of development of frog's eggs. The addition of acid to such water releases free carbon dioxide and this may have been the accelerating agent. Bellamy did not place eggs under experimental conditions until the 2 to 4-celled stages and observed acceleration in the acidified water by the gastrula stage which was increased by the neural fold stage. It is worth noting that we have preliminary evidence which suggests that an increase in carbon dioxide from well below up to full atmospheric equilibrium, which in our experiments was about 0.5 cc. per liter, may speed up the closure of the yolk plug; at least we have no evidence that such an increase slows down this process as it has been found to retard early cleavage. It may be significant in this connection that Ryan ('41) found that the time-temperature relation of cleavage, although constant from first to fourth cleavages, differs from that of embryo formation.

Vernon's ('95) results with Strongylocentrotus plutei deserve more than the passing mention given in an introductory paragraph of this paper. He found that the body length was increased with small increases in carbon dioxide. It appears that he obtained an increase in body size using up to about 15 per cent of saturation. A larger increase was slightly depressing and, relatively suddenly, further increases became completely inhibiting to development. Rapkine and Prenant ('25) found that carbon dioxide was used in the formation of spicules by plutei and this, rather than protoplasmic stimulation, may account for the results reported by Vernon.

The most convincing evidence of the existence of an optimum concentration at some point above the minimum comes from the growth of bacteria (Buchanan and Fulmer, '30). Even small traces are important and perhaps essential (Valley and Rettger, '27; Gladstone, Fildes and Richardson, '35). Also Walker ('32) and others have evidence that the lag phase in bacterial population growth is related to the time taken to build up the proper tension of carbon dioxide. The optimum tension for bacteria varies tremendously with different species. Rahn (1941a) has recently reported that bacteria need carbon dioxide not only during the lag phase but also in the period of rapid growth. Their metabolism is so great at this stage, however, that with species which produce carbon dioxide as a metabolic product, its need can be conclusively demonstrated only when very few cells are inoculated. Species which do not produce carbon dioxide, *Streptococcus lactis* for example react more promptly to its removal. Rahn also found (1941b) that pure cultures of an alga, Chlorella sp., and of two colorless flagellates, *Polytomella caeca* and *Astasia longa,* did not grow nearly so well, if at all, in small cultures without carbon dioxide as they did in a normal atmosphere. He states that the reason is unknown.

With higher plants, Hamon ('36) found that the tissues of different plants respond differently to marked increases in carbon dioxide tensions so far as rate of oxygen consumption is concerned. Some showed no response, others increased and still others decreased their oxygen intake with higher tensions of carbon dioxide.

In studying the oxygen consumption of planarians Hyman ('25) usually found depression with increased carbon dioxide tension though, under certain conditions, a doubtful acceleration was obtained. Hyman (p. 309) recognized that the evidence for stimulation was not convincing. Root ('30) using Paramecium, also found a slight increase in oxygen consumption correlated with relatively small increases in carbon dioxide. While consistent, the increase "probably lies within the experimental error." If it is real, Root suggests that the increase in oxygen uptake is a result of increased motility of Paramecium induced by carbon dioxide.

The experiments recorded in the present paper, when considered in connection with those in the pertinent literature, do not allow a generalization to be made concerning the physiological effect to be expected from relatively small increases in carbon dioxide tension such as occur in and near aggregations of animals or of their eggs. The stimulating effect of increased carbon dioxide upon the rate of external respiratory movements of vertebrates and insects is well established for many forms. With this exception, the physiological accelerations which frequently result when animals aggregate, cannot reasonably be attributed to stimulation by carbon dioxide without experimental demonstration.

SUMMARY

1. Under the conditions tested, any increase in carbon dioxide tensions from nearly complete abscence to the highest amount tested (53.3 cc. per liter) retarded the rate of early cleavage of frog's eggs.

2. Grouped eggs were less affected by such small changes in carbon dioxide tension than were isolated eggs.

3. Heightened activities which frequently accompany animal aggregations cannot be attributed to stimulation from a slight increase in carbon dioxide without experimental demonstration that this is actually the stimulating agent.

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A POLLEN STUDY OF A SUBALPINE BOG IN THE BLUE MOUNTAINS OF NORTHEASTERN OREGON[1]

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INTRODUCTION

This is one of a series of studies on post-Pleistocene vegetation history and general climatic trends in the Pacific Northwest. The forest succession is interpreted from pollen profiles of peat bogs and lake sediments. Bogs are common in some parts of this region, whereas in others they are few and widely scattered. Peat profiles from many of the vegetation and climatic provinces of this vast region have been analyzed, and it is hoped that one or more profiles may be obtained from each plant association. In some cases it has been possible to obtain only a single peat profile from an extensive association. The pollen profiles of one bog may not portray adequately the vegetation history of an entire association, but the correlation of profiles from several should tend to substantiate or refute the evidence offered by a single bog. Pollen profiles of most bogs thus far studied show a fair degree of correlation, with the exception of those located in areas where a pumice mantle has been the major control of forest succession. The vegetation history has been interpreted from the pollen profiles of bogs located in the following associations: The hemlock-cedar of the Puget Lowland and southwestern British Columbia, the spruce-hemlock of the Olympic Peninsula and Oregon coast, the larch-pine of central, north central, and northeastern Washington, the hemlock-cedar-lowland white fir of northern Idaho, the pine-Douglas fir on the eastern slope of the Oregon Cascades, and the pine-hemlock about Crater Lake, Oregon. Bogs located in the Willamette Valley of western Oregon and the sagebrush areas of eastern Washington and the northern Great Basin of southern Oregon have also been analyzed. The bog of this study is of especial interest because of its high elevation. To the author's knowledge it has the greatest altitude of any bog analyzed.

In alpine and subalpine lakes of the Pacific Northwest, hydrarch succession has rarely progressed to a stage of sufficient organic sedimentation to warrant pollen analyses. It seems probable that the short growing season, the severe winters, and the low water temperature are the chief reasons for the comparative absence of peat. Another consideration is the youthfulness of the lakes, due, perhaps, to the persistence of mountain glaciers for a longer period of time than the continental ice sheet at lower elevations. The absence of peat-forming plants may be another factor in the slow rate of peat accumulation.

LOCATION AND CHARACTERISTICS OF THE BOG

The site of the peat deposit is Mud Lake, one of the Anthony Lakes that lie near the crest of the Blue Mountains in northeastern Oregon. It is about 25 miles northwest of Baker, in section 7 of T. 7 S., R. 37 E. on the Sumpter Quadrangle. The altitude is about 7000 feet. The lake has been ponded in a glacial valley less than two miles from the headwaters of Anthony Fork River, the upper tributaries of which rise in a series of cirques at the bases of three peaks that attain an altitude of more than 8000 feet. The lake is only a few acres in extent and very shallow. The author was unable to determine whether it was formed in a kettle or dammed by a terminal moraine. A considerable portion of the lake is occupied by a submerged hydrosere. Near the shore a floating stage consists chiefly of pondweed (*Potamogeton* sp.). A zone of sedge (*Carex* spp.) from 50 to 100 feet wide surrounds much of the lake.

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[1] Published with the approval of the Monographs Publication Committee, Oregon State College, as Research paper No. 71, School of Science, Department of Botany. The expenses of this project were defrayed by a grant-in-aid from the General Research Council, Oregon State College.

Peat samples were obtained at two places near the shore in the sedge zone at 2-decimeter intervals, with a Swedish-type peat borer. The depth of one profile is four meters, while that of the other is three meters. The organic sediments are underlain with volcanic ash which was impenetrable to a depth greater than six inches. Additional peat strata may underlie the ash, but the depth of the profile at this altitude suggests that it represents most, or all, of post-Pleistocene time. The source of the ash is unknown. The occurrence of a single layer of ash is common in post-Pleistocene bogs in Washington, both east and west of the Cascade Range (Hansen, '38, '39a, '39b, '40a, '41a, '41e, '41f; Rigg and Richardson, '38). Pumice strata are present in peat profiles in the Willamette Valley and Cascades of Oregon (Hansen, '42b, '42c, '42d). The ash in Washington bogs probably came from Glacier Peak in the northern part of the State (Hansen, '41f). Other possible sources are Mt. St. Helens, Mt. Adams, and Mt. Baker. The pumice strata in peat profiles of the Willamette Valley evidently came from the eruption of Mount Mazama, about 5000 years ago, which formed the caldera holding Crater Lake in southern Oregon (Williams, '41). In a montane bog near Bend, Oregon, there are two strata of pumice, separated by 2.5 meters of organic sediments (Hansen, '42c). The upper layer undoubtedly had its source in the eruption of Mount Mazama, but the source of the lower stratum is unknown. Peat deposits nearer to Crater Lake are underlain by several feet of Mount Mazama pumice (Hansen, '42d). In other parts of northeastern Oregon, a layer of volcanic ash[2] is exposed several feet below the surface of recent wash in gullies. It is not possible at present to say if this ash is synchronous with that underlying the peat deposit of this study. It is possible that the latter was transported into the lake by streams that cut into older ash deposits. This theory is somewhat supported by the abundance of pollen within the ash stratum itself. Volcanic glass is present in diminishing quantity upward in the profiles, indicating continued transportation of the ash. Brown sedimentary peat overlies the ash stratum and grades upward into fibrous peat near the surface.

METHODS

In preparation of the sediments for microscopic analysis, the potassium hydrate method was used. One hundred and fifty to 200 pollen grains were identified from each level. The identification of the winged conifer pollen was based upon the size-range method (Hansen, '41a, '41b, '41d). In this study pollen listed as that of whitebark pine (*Pinus albicaulis*) may include some of the western white pine (*P. monticola*) and limber pine (*P. flexilis*), because the size-range in these species lies within that of whitebark pine. Western white pine is present in the Canadian life zone of the Blue Mountains, but limber pine occurs only in the Wallowa Mountains of northeastern Oregon and probably is not represented here (Munns, '38). It may, of course, have existed abundantly in the past. Pollen listed as that of alpine fir (*Abies lasiocarpa*), may include a trace of lowland white fir (*A. grandis*). Species that are recorded to 1.5 per cent or less are listed in the tables as 1 per cent.

The interpretation of vegetation history from pollen profiles involves a number of errors, both obvious and intangible. Interpretation of climatic trends is also subject to sources of error involved in the relative climatic indicator evaluation of the several species concerned. One of the sources of error in interpreting forest succession from pollen profiles is the factor of relative abundance. It is assumed that an increase in the pollen proportions of one species and a decrease in those of another denote a correlative change in their actual abundance. It is possible, however, that one species or group of species may increase in abundance while another remains static, or vice versa, although the latter shows a decrease in pollen proportions. In this study the presence of pollen from species of several life zones tends to amplify the importance of relative abundance.

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[2] Personal communication from J. E. Allen, Geologist, State Department of Geology and Mineral Industries, Portland, Oregon.

FORESTS IN ADJACENT AREAS

The site of the peat profiles lies within and near the upper limits of the Hudsonian life zone (Bailey, 1936). A few miles to the south of Mud Lake, the Hudsonian grades into the Arctic-alpine zone. The highest peak in the latter zone is Rock Creek Butte with an elevation of 9097 feet. The Canadian zone surrounds the Hudsonian at lower altitudes, and in turn the Canadian gives way to the timbered Arid Transition. The bog is located in the Petran subalpine forest association according to the classification of forest climaxes by Clements (Weaver and Clements, '38). The typical dominants of this association in the Blue Mountains are alpine fir, whitebark pine, and Engelmann spruce (*Picea engelmanni*). Whitebark pine occurs abundantly near timberline. Lodgepole pine (*Pinus contorta*) is the most abundant species in both the Canadian and Hudsonian zones, occurring as a subclimax due to fire (Clements, '10). A cursory survey suggests that about 50 per cent of the forests in the vicinity of the bog consists of lodgepole pine, 25 per cent of alpine fir, and 25 per cent of Engelmann spruce. These species are present in mixed stands. Species common in the Hudsonian zone of the Cascades such as Alaska cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), and alpine larch (*Larix lyallii*) are absent or rare in the Blue Mountains. A few pollen grains of mountain hemlock are present in the peat profiles, and this species was observed in this part of the Blue Mountains by Sudworth ('08). In the Canadian zone, lodgepole pine probably composes a greater proportion of the forest than in the Hudsonian zone. Engelmann spruce is also common in the upper part of the Canadian zone. Other species of greater or lesser abundance in this zone are Douglas fir (*Pseudotsuga taxifolia*), western larch (*Larix occidentalis*), western white pine, and lowland white fir. Western hemlock (*Tsuga heterophylla*) is of rare occurrence in the Blue Mountains and was not noted by Sudworth ('08), although Munns ('38) shows a single station for this species. It has existed within range of pollen dispersal to the site of the bog, however, because it is sparsely and sporadically recorded by its pollen in both of the profiles (tables I and II). Two other species, common in the Canadian zone of western Oregon and Washington but seemingly absent from the Blue Mountains, are noble fir (*Abies nobilis*) and silver fir (*A. amabilis*).

The timbered Arid Transition area is narrow and the principal species is western yellow pine (*Pinus ponderosa*). Yellow pine forests are far more extensive at lower elevations to the west than to the east, where they form only a narrow zone between the Canadian and timberless Arid Transition. In the upper part of this province, a few specimens of white fir (*Abies concolor*) are to be found. Douglas fir, western larch, and lowland white fir are also present on favorable sites. The principal broadleaf species in this zone is black cottonwood (*Populus trichocarpa*), which thrives along water courses. In the Canadian zone, aspen (*Populus tremuloides*), mountain alder (*Alnus tenuifolia*), and mountain maple (*Acer douglasii*) grow in restricted areas.

CLIMATE

The bog is located within a climatic province designated as semi-arid, microthermal, and with a deficiency of precipitation at all seasons (Thornthwaite, '31). The forests of the Canadian and Hudsonian zones, however, prove that there is sufficient precipitation for tree growth. The mean annual precipitation at Columbia Mine, 10 miles to the southeast, is about 35 inches; at Greenhorn, 18 miles to the southwest, it is also about 35 inches; and at Ibex Mine, 10 miles to the south, it is 29 inches (Climatic Summary, U. S. D. A., '36). At all three stations, between 20 and 23 per cent of the annual precipitation occurs from May to September inclusive. Their elevation is about 6000 feet, and the precipitation is probably similar to that in areas adjacent to the bog. At Baker, with an elevation of 3500 feet, the mean annual precipitation is almost 12 inches, with 35 per cent occurring from May to September. The mean annual precipitation at Seattle, Washington, in the midst of the hemlock-cedar climax is about 33 inches, with only a small percentage occurring from May to September. It seems probable that the more rigorous climate due to greater altitude is responsible for the relative absence of western hemlock and Douglas fir in the Anthony Lakes region.

VEGETATION HISTORY

The forests within range of pollen dispersal to Mud Lake when the lowest pollen-bearing sediments were deposited, consisted chiefly of whitebark, lodgepole, and western yellow pine. The first two are recorded to 42 per cent in the deeper profile and to 38 and 40 per cent respectively in the other. Lodgepole and whitebark pine are recorded in equal abundance, but the first produces more pollen than other Pacific Northwest conifers, and is undoubtedly over-represented in most peat profiles. Whitebark pine may actually have been more abundant than lodgepole in the Hudsonian zone. Lodgepole declines from the bottom in both profiles to its lowest proportions at 2.8 and 2 meters with 24 and 20 per cent respectively (figures 1, 2). Whitebark pine also declines but remains more abundant than lodgepole to a point about half-way up the profiles, where it is superseded by lodgepole pine. The latter remains predominant to the sur-

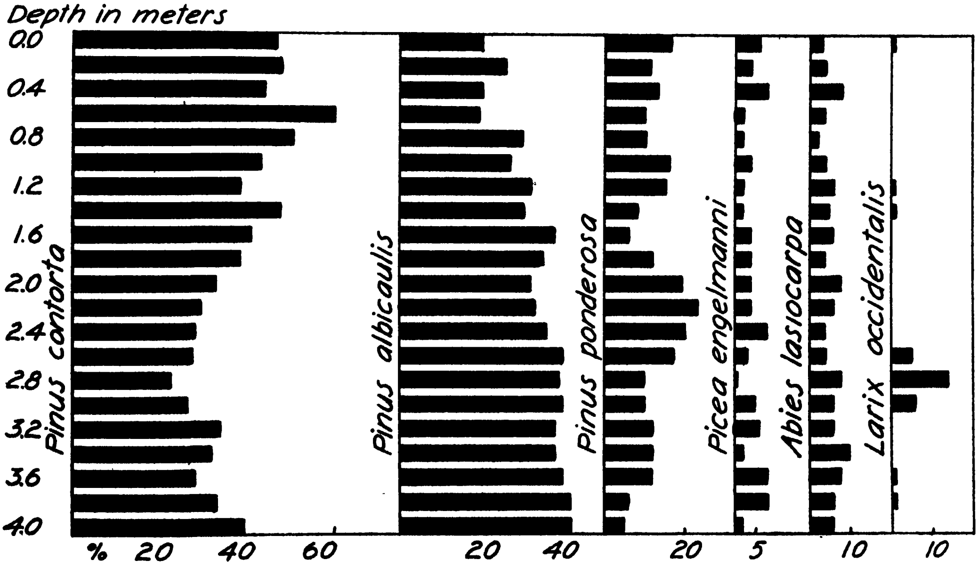

FIG. 1. Pollen profiles, Anthony Lakes, Oregon.

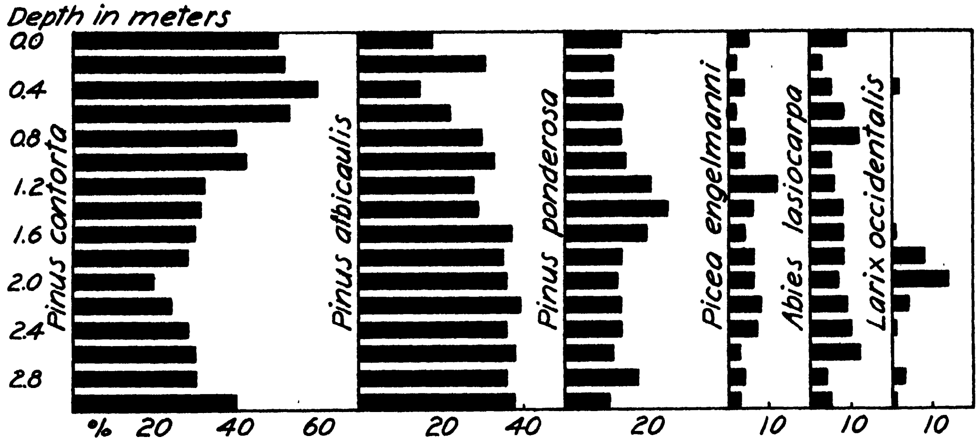

FIG. 2. Pollen profiles, Anthony Lakes, Oregon.

face and whitebark pine continues its general decrease to the surface.

The pollen profiles of western larch are significant. It is sparsely represented in the lower horizons and then shows a sharp increase to 14 per cent at 2.8 meters in the deeper profile and to the same proportion at 2 meters in the other (figures 1, 2). These levels are evidently approximately synchronous. Larch then declines to only a trace and is sparsely and sporadically recorded to the surface in both profiles. Lodgepole reaches its lowest proportions at the levels of larch maximum, and then shows an almost constant increase to the surface. The influx of larch suggests the occurrence of several fires in close succession. This species has very thick bark, and is able to survive severe fires that first destroy the parent trees of other species, and then the seedlings (Sudworth, '08, Larsen, '29). Larch then flourishes in the absence of competition with other tree species. If the area is undisturbed by fire, however, other species will gradually replace larch because of its intolerance of shade. Lodgepole may also benefit from fire, but in a different way. Many of its cones do not open when mature, but cling to the tree for many years, retaining viable seed. The heat from fire may cause the cones to open, shedding considerable seed. The absence of competition likewise permits this pine to thrive until others regain a foothold and gradually replace it (Harlow and Harrar, '41). The decrease of lodgepole to the level of larch maximum suggests that it also suffered from the hypothetical fires. Its rapid increase from this level to the surface, however, indicates that the environment was favorable from that time to the present (figures 1, 2). An initial predominance of larch recorded in the peat profile near Bend, Oregon, also denotes repeated fire prior to sedimentation (Hansen, '42c). Larch does not shed nearly so much pollen as the pines, and it is thus under-represented.

The pollen profiles of yellow pine reveal that the abundance of this species remained static to the time of larch maximum. It fluctuates between 5 and 12 per cent in the deeper profile, and from 11 to 18 per cent in the other. Yellow pine then sharply increases to attain its maximum proportions of 23 per cent at 2.2 meters in the deeper, and 25 per cent at 1.4 meters in the other profile. It declines through the next several levels and remains rather constant to the surface. Apparently the hypothetical fires did not affect the abundance of yellow pine, as it may have existed at lower altitudes and was not subject to fire. Drying of the climate may have been involved in yellow pine attaining its maximum. The horizons of yellow pine maximum in the two profiles are probably synchronous.

Other conifers recorded by their pollen in appreciable proportions are Engelmann spruce and alpine fir. They are represented as having been constant throughout both profiles and show no successional trends. Engelmann spruce fluctuates between 1 and 12 per cent, while alpine fir varies from 2 to 12 per cent in the two profiles. Fire evidently prevented these species from reaching their greatest development. Douglas fir, western and mountain hemlock, and white fir are also represented in low proportions (tables I and II). Pollen of broadleaf species present includes chiefly alder and maple, with the latter most abundant. Composites, grasses, and chenopods are sparsely but consistently represented. The pollen of chenopods may have come from dryer and alkaline areas at much lower elevations.

In most post-Pleistocene peat profiles located within the glaciated region of the Pacific Northwest, lodgepole is recorded as having been the chief pioneer invader (Hansen, '38, '39a, '39b, '40a, '41a, '41e). Peat profiles in the lower Willamette Valley of Oregon also show lodgepole pine as the pioneer postglacial invader, though it is entirely absent in this area at present (Hansen, '42b). The Willamette Valley was not glaciated but it was inundated by glacial backwater from the Columbia River (Allison, '35). The unstable physiographic and edaphic conditions during the early post-Pleistocene were probably responsible for the initial predominance of lodgepole here and in many other parts of the Pacific Northwest. The advantage obtained by lodgepole pine due to radical changes in the edaphic conditions is well exemplified by a pollen study of a 7-meter pollen-bearing profile on the east slope of the Cascade Range, near Bend, Oregon (Hansen, '42c). Two strata of pumice occur in the profile; one at 4.5 and the other at 2 meters. The pumice mantle deposited by the earlier volcanic eruption interrupted a strong trend toward a yellow pine climax, which is the normal climatic climax of this region. Lodgepole is recorded as having made a sharp increase to assume predominance immediately after the eruption. As the pumiceous soil was somewhat modified, yellow pine partially regained its former abundance, only to be interrupted again by the second volcanic eruption. Lodgepole maintained predomi-

TABLE I. *Percentages of fossil pollen. Anthony Lakes.*

Depth in meters	4.0	3.8	3.6	3.4	3.2	3.0	2.8	2.6	2.4	2.2	2.0	1.8	1.6	1.4	1.2	1.0	0.8	0.6	0.4	0.2	0.0
Pinus contorta	42	35	30	34	36	28	24	29	30	31	35	41	44	51	41	46	54	64	47	51	50
P. albicaulis	42	42	40	38	38	40	39	40	36	33	32	35	38	30	32	27	30	19	20	26	20
P. ponderosa	5	6	12	12	12	10	10	17	20	23	19	12	6	8	15	16	10	10	13	11	16
Pseudotsuga taxifolia	1	1	1	2	2	1	1	1	1	1				1	1		1		1	1	1
Tsuga heterophylla	1					1			1	1		1	1					1	1		1
T. mertensiana	1	1		1		2	1				1	1	1		1	1			1	1	1
Picea engelmanni	2	8	8	2	6	5	1	3	8	4	4	4	4	2	2	4	2	2	8	4	6
Abies lasiocarpa	6	6	8	10	6	6	8	4	4	6	8	4	6	5	6	4	2	4	8	4	3
A. concolor				1		1	2	1		1	1	2		2	1	2	1		1	2	1
Larix occidentalis		1	1			6	14	5						1	1						1
Pinus spp.*	12	17	17	15	21	12	15	22	21	23	22	17	10	20	17	19	20	18	17	19	15
Abies spp.*	1			2		1				1	1										1
Gramineae*		1	2	1		1	2	1					1	2		1					2
Compositae*	1		3	2		3	2	4		2	2	2			4				1		1
Chenopodiaceae*	1	1	1		1	1	1		2	2	1		2	2		1		1			
Alnus*	3		2	3		1		3						1	1	1	1	1			1
Acer*	6	8	6	4	3	7	2	4		6	3	3	4	4	2	5	2	2	5	1	6
Salix*					5		1				1	1		1						1	
Cyperaceae*	2	2	3	5	1	5		1	2	1	2	2	6	1	7	4	2	1	4	1	65
Nymphozanthus*			1	1	2	3	2	4	1			1	1	1	1					1	1

* Number of pollen grains, not computed in the percentages.

TABLE II. *Percentages of fossil pollen. Anthony Lakes.*

Depth in meters	3.0	2.8	2.6	2.4	2.2	2.0	1.8	1.6	1.4	1.2	1.0	0.8	0.6	0.4	0.2	0.0
Pinus contorta	40	30	30	28	24	20	28	30	31	32	42	40	53	60	52	50
P. albicaulis	38	36	38	36	39	36	35	37	29	28	33	30	22	15	31	18
P. ponderosa	11	18	12	14	14	13	14	20	25	21	15	14	14	12	12	14
Pseudotsuga taxifolia	1	3	3	3		1	1			1	1		1	1		1
Tsuga heterophylla					1	1										1
T. mertensiana	1		1	1	1	1										
Picea engelmanni	3	4	3	7	8	6	6	4	6	12	4	4	2	4	2	5
Abies lasiocarpa	5	4	12	10	9	7	8	8	8	6	5	12	8	5	3	9
A. concolor		2	1			1			1					1		2
Larix occidentalis	1	3		1	4	14	8	1						2		
Pinus spp.*	12	15	11	11	12	17	15	16	22	21	15	18	19	15	23	17
Abies spp.*			2		1	1	3			1						
Gramineae*		1									1					
Compositae*		1	1		1	1	1	1	3	1			1		1	1
Chenopodiaceae*		1		1	1		1			3	1	2	2			2
Alnus*			3	1	1	1	3									
Acer*		6	6	9	4	7	5	1	4	1	5		2	8	2	1
Salix*				1		2		3		1		3		1		1
Cyperaceae*			1	2	2		3	2	3	3	2	2	3	3	12	42
Nymphozanthus*				1	3	3	1		1							

* Number of pollen grains, not computed in the percentages.

nance to the present. The vast lodgepole pine forests on the pumice mantle of central Oregon have existed as an edaphic climax since the first recorded post-Pleistocene volcanic eruption. In unglaciated regions where the forests and soil were not materially disturbed during the later part of the Pleistocene, or the early part of the postglacial period, pollen profiles show that lodgepole was not predominant when the earliest sediments were deposited (Hansen, '41b, '41c, '41d). Usually the dominants of the present formations are most abundantly recorded throughout the profiles.

CLIMATIC CONSIDERATIONS

The chief climatic indicators are whitebark and yellow pine. The first exists at and near timberline in the Hudsonian zone and the latter thrives in the timbered Arid Transition. These two provinces are separated by the Canadian zone, but no species characteristic of this zone are recorded in significant quantity. Undoubtedly the pollen listed as that of whitebark pine includes some of western white pine. The latter is a good indicator of the Canadian zone in the Pacific Northwest, and it may have been more abundant in the Anthony Lakes region during the past. Engelmann spruce also grows largely in the Canadian zone, but its pollen proportions are too low and its profiles too constant in this study to mark any climatic trends. The most common tree by far in the Canadian zone is lodgepole, and it is of little value as a climatic index. Western larch grows in the upper part of the Transition and the lower part of the Canadian, but this species is rarely predominant, except as a result of repeated fire. The pollen profiles of alpine fir are too constant and its proportions too low to warrant a climatic interpretation. The pollen of Douglas fir, white fir, and western and mountain hemlock is too scanty in both profiles to offer any evidence for climatic trends.

Western yellow pine is perhaps the best climatic indicator. It is one of the most xerophytic of Pacific Northwest conifers, and because of its existence adjacent to the low elevation timberline, its response to climatic changes should be reflected in the pollen profiles. It would seem that whitebark pine is also a good climatic indicator, because it exists adjacent to the high elevation timberline. It is especially significant in this case since the bog is located near the upper limits of the Hudsonian zone, immediately below timberline. The high proportions of lodgepole pine, however, tend to minimize the climatic indicator value of whitebark pine in these profiles. The rapid gain in yellow pine from the horizon of larch maximum in both profiles, signifies a warming and drying of the climate as the influence of recent glaciation waned. The larch maximum suggests that fire retarded the trend of yellow pine increase. As the effects of the hypothetical fires were modified, yellow pine belatedly responded positively to the warming climate. The general decline in whitebark pine from the bottom to the level of yellow pine maximum is corroborating evidence for this climatic trend. The decline of yellow pine from its peak to proportions that are generally maintained to the surface, marks a cooling and humidifying of the climate to a degree which has persisted to the present. A continued decline in whitebark pine from the time of yellow pine maximum almost to the present, however, does not substantiate this interpreted trend. The rapid gain of lodgepole from the time of larch maximum to nearly the present denotes a sustained favorable environment for this species in the Canadian and Hudsonian zones. The recorded decline of whitebark pine during the same period may then be merely relative. It probably remained more or less constant in the upper part of the Hudsonian zone.

Yellow pine pollen preserved in the sediments must have come from forests at much lower elevation. This means that the factor of relative abundance may be of critical importance. Does the increase in yellow pine pollen proportions denote an upward movement of the timbered Arid Transition due to a warming and drying of the climate, an increase in yellow pine within its own province because of non-climatic changes in the environment, an increase in relative abundance, or merely an alteration of those factors controlling the transportation and preservation of the pollen in the accumulating sediment? Notwithstanding these possibilities, the occurrence of a post-Pleistocene xerothermic period as portrayed by the yellow pine profiles of this study is substantiated by pollen profiles of other peat deposits in the Pacific Northwest, both east and west of the Cascade Range. In some profiles the recorded succession of grasses, composites, and chenopods marks the period of desiccation, while in others the trend of forest succession depicts a gradual warming and drying to a maximum, succeeded by cooling and humidifying to a degree that has been maintained to the present (Hansen, '39b, '40b, '41b, '41e, '42a). In the Willamette Valley of western Oregon a partial replacement of Douglas fir by white oak (*Quercus garryana*) in the upper one-third of three peat profiles supports the interpreted occurrence of a xeric period (Hansen, '42a). Anthropological and geological studies in southcentral Oregon also tend to corroborate the evidence offered by the pollen profiles (Cressman, '40; Antevs, '40).

SUMMARY

A pollen study of a subalpine bog in the Blue Mountains of northeastern Oregon suggests that changes in relative abundance of the several species of forest trees may have been an important factor in determining their pollen profiles. The tree pollen of three life zones is preserved in the peat profiles. The Hudsonian zone, in which the pollen-bearing sediments are located, is the best represented, with lodgepole and whitebark pine predominant. The Canadian zone is poorly represented by a typical species, but lodgepole pine has probably been abundant in this zone also, because of fire. The timbered Arid Transition is represented by western yellow pine.

Whitebark pine shows a general decrease from the bottom to the surface. This indicated trend may be merely relative because of an increase in actual abundance of lodgepole pine in the Hudsonian and Canadian zones. Lodgepole pine manifests its predominance in the upper half of the profiles. Although lodgepole probably owes its abundance to fire, its initial decline and the concurrently sharp increase of western larch to its maximum in the lower third of the profiles, marks the occurrence of repeated fire, too severe even for lodgepole. Generally constant proportions of yellow pine during this period indicates that the fires did not occur in the Arid Transition. Its increase from the level of larch maximum and lodgepole pine minimum denotes warming and drying of the climate. A decline of yellow pine immediately following its peak denotes an increase of moisture to a degree which has persisted to the present, or merely a change in relative abundance. Engelmann spruce and alpine fir are recorded in low proportions, reflecting the influence of fire in preventing their normal development in this region.

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THE INFLUENCE OF DIFFERENT AMOUNTS OF ILLUMINATION UPON THE BODY WEIGHT OF BIRDS

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It has been known for more than 100 years that the winter egg production of domestic fowl can be increased by providing adequate light (Castello, '24), but no influence of light upon the body weight of birds has hitherto been demonstrated. In a thorough review of available data, Baldwin and Kendeigh ('38) were able to show that several species of passerine birds attain their greatest body weight during the winter and exhibit seasonal changes in weight that are inversely correlated with both environmental temperature and the possible number of hours of sunlight each day. Convincing evidence was given to show that a significant inverse correlation exists between body weight and the environmental temperature, either of the same day or of the previous night. The available data did not permit a clear distinction between the influence upon body weight of seasonal changes in the temperature and in the hours of sunlight each day. However, they expressed a common belief when they assumed that sunlight was not an important cause of seasonal variations in weight because, "if this were true one would expect a positive correlation, not an inverse one. With the longer days for feeding and the shorter warmer nights of summer the bird's weight should increase rather than decrease."

Since seasonal changes in temperature and daily hours of sunlight are interdependent, it is difficult, if not impossible, to distinguish between their effects in a study of data obtained from wild birds living in their natural environment. However, a clear distinction can be made between the effects of temperature and light upon the weight of domestic birds subjected to different periods of illumination daily, but kept under otherwise comparable environmental conditions. This study was undertaken to determine whether or not different amounts of illumination have any influence upon the body weight of White Leghorn males.

MATERIAL AND METHODS

Male fowl were selected for this study because any differences in the influence of different amounts of light upon their reproductive tracts would have somewhat less influence upon their body weights than upon those of females. Although moderate changes in the size of testes in White Leghorns may result from differences in illumination, these differences in weight are much less than those between the reproductive organs of laying and non-laying hens.

Cages. The White Leghorn males considered in this study were kept in laying cages of a standard type during the experimental periods. This was done to provide each male with an equal opportunity to eat, and to avoid deviation from normal growth which might be induced by the psychological reactions within the "pecking order" which prevent equal freedom for eating and drinking and frequently result in injury when males are kept together in pens. Feed and water were available to the birds at all times, and observations indicated that they ate freely during the periods of darkness.

The birds were dubbed (most of their combs and wattles removed) some time before the twelfth week of age. This is essential when males are kept in the standard types of laying cages because the large combs of Leghorn males frequently catch on the bars of the cage and thus discourage the consumption of feed. It has been shown (Lamoreux and Jones, '42) that dubbed and normal males which have comparable weights when kept on the floor with feed in open troughs may be significantly different when kept in cages that interfere with withdrawal of the heads of undubbed birds from the feeders.

The dark pens used for these experiments were six adjoining rooms about 10′ × 14′ in size which were so insulated that light from the outside or from adjacent pens could not enter. Ventilation was controlled by means of electric fans placed in flues constructed to exclude the light. Electric heaters were controlled by thermostats adjusted to furnish heat when the room temperature dropped below 45° F. Usually the temperature did not drop below that level, although during a few nights of severe cold a small amount of ice formed in the water troughs. The daily periods of artificial illumination were controlled by means of automatic electric time clocks.

Results

Three experiments were undertaken which included 36, 69, and 81 cockerels, respectively, that survived the periods during which illumination was controlled.

Experiment I.—Cockerels for Experiment I were hatched during March, and about the first of June they were removed from the rearing range to be placed in cages in a dark room. There they received less than one hour of light each day (average), just time enough for an attendant to care for their needs. It was believed that the effects of light might be most accurately measured by using experimental birds that had previously received as little light as could readily be arranged. However, it appeared impractical to keep the cockerels in continuous darkness because it would then be difficult to feed and water the birds and to clean the cages. Furthermore, if there is a correlation between the length of the daily period of light and body weight, it is apparent from the data reviewed by Baldwin and Kendeigh ('38) that it is a negative one. This made it likely that if differences of 23 hours of light each day were ineffective in modifying body weight, then a study of any further deficiency of light would be unwarranted.

The following September these birds were distributed at random among six experimental pens. They were then subjected to periods of illumination lasting in the six different groups, less than 1 hour, 9, 12, 14, 16, or 24 hours daily from October 6 to November 9. With 75-watt Mazda lamps in the type of re-

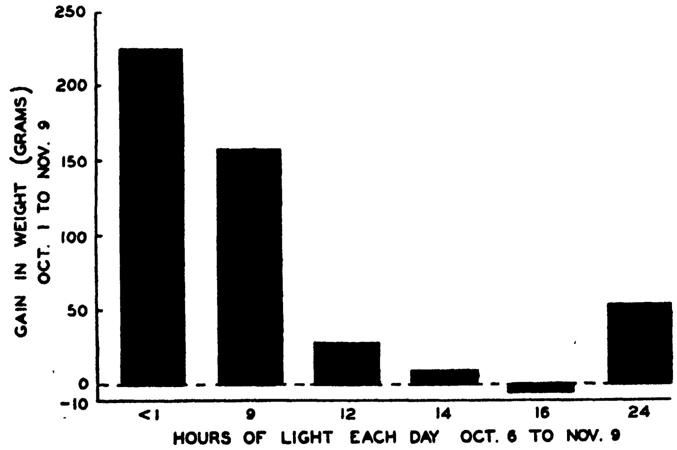

Fig. 1. Gains in the body weight of White Leghorn cockerels when subjected to different daily periods of illumination after a period of four months during which they were exposed to less than one hour (average) of light daily.

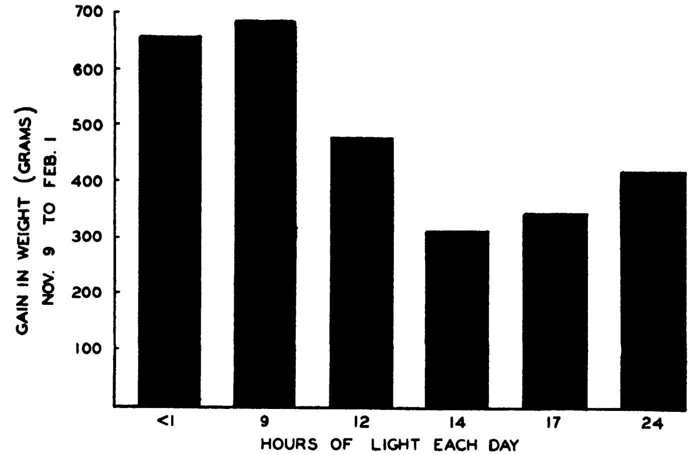

FIG. 2. Gains in the body weight of White Leghorn cockerels when subjected to different daily periods of illumination after removal from a grass rearing range on November 9.

flectors used, the intensity of the light at the position of the birds was approximately 1.6 foot-candles. Since the birds were in cages three decks high, the light was projected upon them horizontally rather than from the ceiling.

During this experimental period of 34 days, the average gain in weight by birds subjected to < 1, 9, 12, 14, or 24 hours of illumination daily was 225, 157, ·26, 7, and 52 grams, respectively. Those cockerels exposed to light 16 hours daily showed an average loss of 5 grams. The males receiving the least light gained weight most rapidly, and figure 1 illustrates the fact that, with the exception of the pen receiving 24 hours of light, the longer the period of irradiation the less the birds gained in body weight.

Further study of these data by means of analysis of variance has shown the odds to be greater than 99:1 that the difference in gain between those birds which received 9 hours or less, and those which received more than 9 hours of light daily is not a result of chance (value for $P = < 0.01$). There was, however, no evidence of any real difference among the four groups that received 12, 14, 16, or 24 hours of light daily.

These results suggest that optimum gains in weight are made when birds are subjected to less than the threshold level of 12 to 13 hours of light daily required to stimulate either spermatogenesis in the starling (Burger, '40) or egg production in the fowl (Roberts and Carver, '41).

Experiment II.—The birds for Experiment II were hatched during March and April, but were not removed from the rearing range until the following November 9 when they were distributed among six pens where they received the same light treatments as did the birds of Experiment I, except that illumination for the pen which received 16 hours of light was increased to 17 hours daily. In this experiment the males were so distributed that the mean weights and their standard deviations in the six experimental groups were very nearly the same. Twelve birds were placed in each pen except that having least light, and it contained 15.

These males, previously very active on their grass range, gained weight under each of the six experimental treatments, but it is apparent from figure 2 that again those birds which received 9 hours of light daily, or less, made greater gains than the others. This difference also is highly significant with odds of more than 99:1 that it could not have occurred by chance.

Further study of the data with analysis of variance did not reveal a difference among pens receiving 12 to 24 hours of light, unless the difference between pens receiving 12 and 14 hours of light (value for $P =$ about 0.04) could be considered significant. Birds receiving 9 hours of light made greater gains in weight than those subjected to 12 hours of illumination, the difference being significant according to the usual criteria (value for $P =$ about 0.02) and also consistent with results obtained in Experiment I.

Experiment III.—To make the relationship between light and body weight still more clear, 84 cockerels hatched during March and April of the following year, were removed from range on December 3 and divided into two equal groups on the basis of body weight. One male died during the experiment so data concerning him have been omitted.

One group of cockerels was exposed to 14 hours of light daily, the other to only 4 hours. The 4-hour exposure was chosen because it was intermediate between the two periods, 1 and 9 hours, that had resulted in the best gains in weight during previous experiments. The 4 hours of illumination were furnished during two different periods each day, 2:00 A.M. to 4:00 A.M. and an additional 2 hours sometime between 10:00 A.M. and 4:00 P.M., depending upon the time available for the care of the birds.

These males were weighed each week during the following six weeks to determine how the two groups differed during that time with respect to gain in weight. In figure 3, the accumulated average gain in weight of the males receiving least light is shown to be consistently greater throughout the experiment. This difference was highly significant (value for $P = < 0.01$) after only three weeks of experimental treatment. By the end of the experiment, the males receiving 4 hours of light daily had gained 233 grams in weight, whereas those lighted for 14 hours gained 133 grams, only slightly more than half as much.

The consistent results obtained in these three experiments show clearly that when White Leghorn males are held in cages with feed available at all times they gain weight much more rapidly if they receive 9 hours of light daily or less, than if they received 12 hours of light or more.

DISCUSSION

It is now clear that short daily periods of light, such as those which occur in mid-

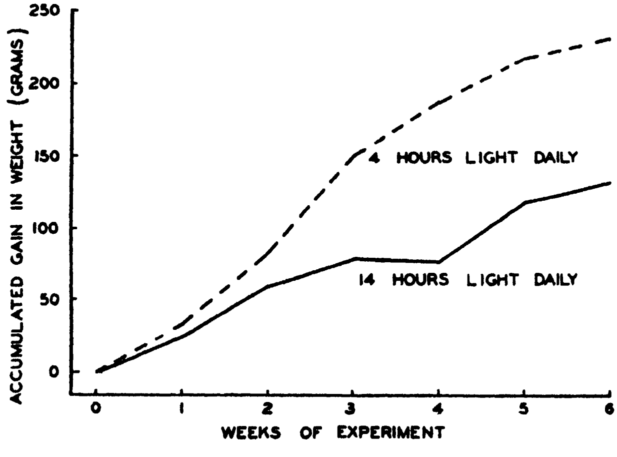

FIG. 3. The accumulated weekly gains in the body weight of White Leghorn cockerels removed from a grass rearing range on December 3, and subjected to different daily periods of illumination.

winter, and shorter than those required to stimulate reproduction, result in significant gains in the body weight of White Leghorn males. It seems likely that this effect upon the fowl is not a peculiar characteristic of that species only, but is a contributing cause of the relatively heavy body weight attained by wild birds during the winter season. The economic importance of such a relationship is apparent when one considers the crises encountered by wild birds during periods of severe cold or shortage of food when reserves of body fat may determine life and death.

We can no longer assume that long daily periods of light are favorable to gains in body weight because they provide increased time for feeding. During periods when food is scarce, it will obviously require more time for wild birds to provide their requirements than when food is plentiful. It is equally obvious, however, that for wild birds which attain their maximum weight during the winter season, even the shortest days of winter furnish adequate time for collecting the food necessary to attain such weight. This was graphically shown by Baldwin and Kendeigh ('38, text figure 4) to be true for several species of passerine birds, despite the fact that such birds are handicapped by lack of a typical crop in which to store food for digestion during the night.

So far as is known, no laboratory experiments with these species have been designed to measure the influence of length of day upon body weight when environmental temperature is controlled and natural foodstuff is available in "normal" abundance. However, data from an experiment designed by Kendeigh ('41, table 2) for another purpose indicate that the English sparrow attains greater body weight during a period of normal winter daylight than when provided with 15 hours of light daily for about four weeks. The environmental temperature was 72° F. for each group. The data given are a summary of several experiments including 62 birds with unrestricted food. The males and females exposed to only normal periods of light weighed 2.6 and 3.9 per cent, respectively, more than birds of their own sex subjected to 15 hours of light daily. These differences are not large, but they exceed the average monthly changes in the body weight of wild passerine birds studied by Baldwin and Kendeigh ('38, text-figure 4) and are consistent in showing the same relationship that has been shown to exist in the fowl between the number of hours of light each day and body weight.

Evidence that this relationship in the fowl is independent of the time required for feeding, even when the periods of natural sunlight are shortest, is found in studies of the time required for laying hens to consume enough feed to sustain a high level of egg production. It seems still to be a popular, but none-the-less erroneous belief that stimulation of egg production in domestic fowl by lengthening the daily period of light is the result of providing more time to eat and drink. That additional time for eating is not important was shown by Dakan ('34) when his White Leghorn hens that received no feed during periods of supplementary illumination showed an increase in egg production comparable to those which had feed available throughout the day. That even the shortest periods of daylight during the winter are more than adequate for the consumption of feed necessary to maintain good egg production was shown by Burmester and Card ('39). Their hens which received an all-mash diet were able to consume the required feed during six consecutive hours of light daily. Other hens receiving the same diet, except that it was compressed into pellets, were able to maintain good egg production when they had feed available only two consecutive hours daily. It seems likely that comparable periods of time should be adequate for non-laying fowl to consume the food required to gain in body weight.

Available evidence does not indicate whether the increased body weight associated with shorter daily periods of illumination results from some hormonal change or merely from longer periods of physical inactivity associated with the longer periods of darkness.

The fact that domestic fowl attain their greatest body weight when the daily periods of light are relatively short is of obvious importance to all students of avian physiology and ecology, but to those concerned with the production of gallinaceous birds it also offers aid in the solution of important economic problems. To maintain prospective breeding males in better flesh, to obtain more rapid and therefore presumably more economical gains in the weight of mature birds intended for market, and perhaps to facilitate recovery of good physical condition in moulting females, a relatively short daily period of illumination will be found useful. The theory that long daily periods of illumination facilitate rapid gains in body weight must be abandoned.

SUMMARY

In each of three experiments, White Leghorn cockerels exposed to light for 9 hours daily, or less, made significantly greater gains in body weight than did birds subjected to 12 hours of light, or more.

Within three weeks after they were removed from range, 42 cockerels exposed to light for only 4 hours daily were significantly heavier than 41 males subjected to 14 hours of light. During the six-week experimental period, the average gain in weight of birds in the two groups was 233 and 133 grams, respectively.

It is clear that gains in the body weight of domestic fowl are greatest when the daily period of light is inadequate for the maximum stimulation of reproduction.

The results also indicate that normal changes in the length of day are a contributing cause of seasonal variations in weight among wild species of birds.

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THE SUCCESSIONAL RÔLE OF SOUTHERN WHITE CEDAR, *CHAMAECYPARIS THYOIDES,* IN SOUTHEASTERN NORTH CAROLINA

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Introduction

A community in which the southern white cedar, *Chamaecyparis thyoides* (L.) BSP., is dominant occurs on peat soils of the Atlantic coastal plain. Such forests are neither common nor extensive in view of the enormous areas of peat land in this region.

The most complete study of southern white cedar is that by Korstian and Brush ('31). This study, together with those of previous investigators, supplied ecological information such as site characteristics, the aspect of the community, associated tree species, and some features regarding reproduction.

The site occupied by the southern white cedar community is consistently peat bog underlain by sand (Korstian, '24; Korstian and Brush, '31). Korstian has pointed out that, with larger proportions of silt and clay in the underlying mineral soil, swamp hardwoods are more abundant. Hardwood-cypress swamps are underlain by clay or sandy-clay subsoil. The aspect of the southern white cedar forest has been described and illustrated adequately. Gifford ('00) gave a description of the community in which he emphasized the extreme density of the forest, the trees growing so close together that they afford mutual support and the bases of the crowns meeting to form a solid canopy. He mentioned the dense undergrowth, but neither he nor any of the other workers has analyzed its composition except to note that it consisted of a dense growth of vines and shrubs. Although Harper ('26) listed associated species of all categories, trees, shrubs, lianas, herbs, and bryophytes in order of their abundance in his account of a middle Florida cedar swamp, the cedars were not the largest nor most conspicuous trees in this community. It must therefore be considered as a mixed bog forest which cannot be compared with the true cedar community. Although Korstian and Brush ('31) found that pure, dense, more or less even-aged stands are most characteristic for the southern white cedar, they listed numerous arborescent associates. The number of associated tree species is greater in the southern part of the range than in the northern part.

It is apparent from the literature that southern white cedar reproduction requires decidedly open conditions. Pinchot ('00) noted that no reproduction occurs after crowns meet to form a continuous canopy. Korstian and Brush ('31) likewise found that seedlings do not tolerate the shade of the cedar forest. They pointed out that, although the seedlings may start under cover of bog shrubs, the shrubs usually develop rapidly into an impenetrable jungle making establishment of the cedar difficult. Ackerman ('23) found that seedlings come up in abundance in the rollways and tramways after logging, but that elsewhere the slash and the rank growth of shrubs and vines produce a mass which the young cedars have small chance of penetrating. This situation was recognized likewise by Korstian and Brush ('31). It is significant in this connection that in New Jersey the southern white cedar constantly invades cranberry bogs (Gifford, '00). Recognizing the requirement for an open seed bed, at least one free from the extreme competition of the bog shrubs and lianas, several authors suggested clearing to obtain reproduction. In view of the dangers involved in controlled burning in such areas, Ackerman ('23) suggested the use of cattle and goats as clearing agents. The effect of fire under various conditions of water table has been investigated by Korstian ('24). In his figure 1, page 189, he showed an instance in the Dismal Swamp where southern white cedar came up after a slash fire during a period of high water table. At such a time fire does not burn the top layer of peat in which there may be stored enormous numbers of viable seeds. In contrast, severe fires when the bog is dry destroy the upper layer of peat and the cedar seeds which are in it. Such conditions favor the development of a hardwood swamp (Korstian and Brush, '31).

The composition of the community as a whole and the rôle of southern white cedar in the dynamics of bog vegetation are subjects which previous studies do not embrace. These features are considered in the present paper.

The forests on which this study is based are located on the coastal plain in the southeastern section of North Carolina. Several stages in the development of the white cedar community are present at Suggs' Pond in Bladen County. The cedars occupy a large peat peninsula that extends into the pond basin. The *initial stage* is represented by an area having abundant seedlings. This is on an extensive bed of peat recently exposed through the draining of the pond. An intermediate stage of young growth occupies an adjacent area which is merely a forest fringe, unsatisfactory for detailed study. It is referred to as the *young forest.* Most extensive and well developed here, however, is a somewhat unevenaged stand averaging 37 years of age. This is referred to as the *middle-aged forest.* Finally, about 60 miles to the southeast in Brunswick County along the upper portion of a tributary of the Waccamaw River is a *mature stand* averaging about 80 years of age. This is located southeast of Lake Waccamaw near the Brunswick-Columbus County line. These forests are all growing on peat seven to eight feet deep underlain by sand, the type of site already noted (Korstian and Brush, '31) as characteristic for southern white cedar. Adjacent to the cedar forests is extensive "pocosin" or shrub bog and since this vegetation type offers considerable competition with the cedar some study has been devoted to it.

METHODS

Samples were obtained with an "American peat borer" (Davis type) at one-foot intervals in the peat and from the underlying sand.

Community composition was studied on plots located at random. For the seedling or initial stage on open peat, five 1 × 1, meter plots were employed. All woody plants were tabulated and notes were made on herbaceous growth. In the forest, both middle-aged and mature, all trees were recorded with diameter measurements on each of ten 10 × 10 meter plots. Age was determined from increment borings taken at random throughout the stands. Seedlings and shrubs were counted on ten 2 × 5 meter plots. For the shrubs, total stems arising from the ground were counted rather than individual plants.

Light measurements with a Weston photometer were taken at random in the shrub pocosin six inches from the ground, the reader crawling carefully through the brush so as not to disturb the shrub canopy. In the forest, readings likewise were taken at random, the reader walking in as straight a line as possible and making a reading at waist height every five paces. Additional readings were made in direct shade of tree trunks, in the text referred to as intensity obtained by full shade sampling. The per cent of light transmitted by the canopy was obtained by referring the readings in the forest and the shrub pocosin to readings for full light intensity in the open. The latter are averages of a set of readings made immediately before and after the determinations in shade.

FIG. 1. Exterior of middle-aged southern white cedar forest at Sugg's Pond. Southern white cedar seedlings had germinated in abundance on the bare peat of the exposed pond bottom in the foreground.

DESCRIPTION OF THE FORESTS

(*a*) *The Initial Stage*

Upon the extensive bed of peat exposed by the recent draining of Suggs' Pond, a mass invasion of seedlings has occurred in the vicinity of the cedar forest (figure 1). This area was studied in December, 1940, about a year and one-half after drainage of the pond had been effected. Scattered trees, especially cypress, had become established before the pond was drained. Aside from these scattered trees the area had assumed more or less the aspect of a depauperate sedge meadow. On the five plots studied in detail there was, in a ground cover of sphagnum, a predominance of the sedge *Dulichium arundinaceum* (L.) Britton, with a few scattered individuals of other species of sedges and grasses. Besides these the following seedlings of trees and young shrubs occurred, the numbers being the total count of all five plots: *Chamaecyparis thyoides,* 53; *Zenobia cassinefolia* (Vent.) Pollard, 14; *Acer rubrum* L., 4; *Vaccinium corymbosum* L., 1; *Leucothoë racemosa* (L.) A. Gray, 5; and *Smilax laurifolia* L., 10. The smilax plants were all seedlings in one clump, in the droppings of a bear.

(*b*) *Young Forest*

Along the margin of the forest and the former shore of Suggs' Pond reproduction has been scattered. The young trees are far apart and as a result there is severe competition between the pocosin shrubs and the cedars. The severest competitor of the young trees is smilax, especially *S. laurifolia*. Great masses of these vines weigh down the tops of many young trees, sometimes even breaking off the trunks (figure 2).

(*c*) *Middle-aged forest*

The trees of the middle-aged forest averaged 37 years old. Light readings in this forest averaged 2.5 per cent and in full shade 1.3 per cent. In places the forest consists of closely spaced trees with straight trunks. Here the crowns meet forming a continuous canopy. Where the trees are more widely spaced there are frequent bent or otherwise deformed trunks which reflect earlier severe competition with smilax (figure 3). About

FIG. 2. The isolated southern white cedar tree has been overrun by *Smilax laurifolia*. Its broken upper part and the mass of vines form a low, flat top in place of a normal spire-like crown.

one small opening in this forest the vines are so rampant that the surrounding trees are being pulled over forming a large wigwam of cedars and smilax vines.

The ground is very uneven. The trees arise from hummocks, between which may be depressions 2–3 feet deep. Long ridges with trees growing on them were found to be fallen cedar logs buried in litter. One such log measured 32 inches in diameter at its largest point. Occasional old, ragged cedar stumps occur. One of these about 8 feet high, fragmented and partially decayed, was determined roughly as 29 inches diameter breast height.

Slightly charred surfaces on the stumps and buried logs are records of a fire that swept through this area. That it was not severe is indicated by a scarcity of charcoal fragments in the upper layer of peat. In fact a scarcity of charcoal in the upper three feet of peat and lack of any charred peat layer denote an absence of severe fire in this area for considerable time past.

In the plot studies the southern white cedar averaged 25 individuals per plot (maximum 39, minimum 15) (table Ia). No other tree species occurred, not even seedlings. The results of the study of understory shrubs also are presented in table Ia. It will be noted that of the six

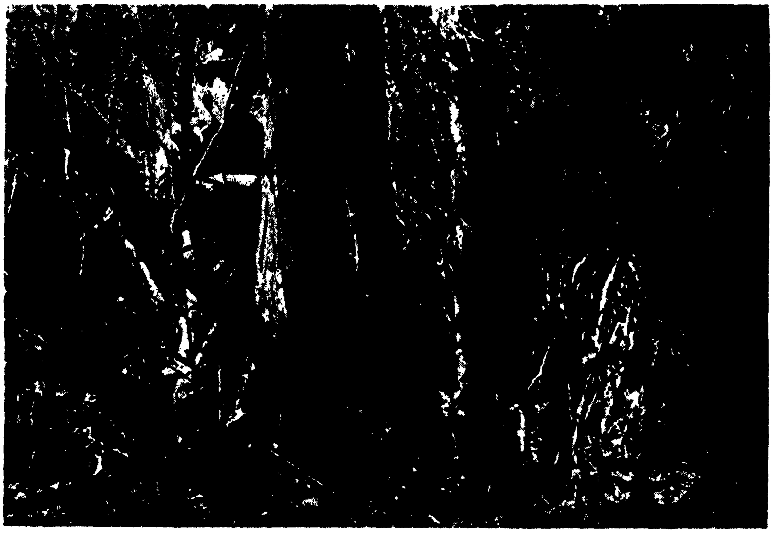

FIG. 3. Interior of the more open portion of the middle-aged cedar forest. Deformed cedars similar to the bent tree on the right indicate development of the forest under more or less open conditions where competition with smilax is severe.

TABLE I. *Comparison of southern white cedar forest areas. Total trees and shrubs per 100 square meters*

Species	Number	
	(a) (Middle-aged (37 yr. old) forest)	(b) (Mature (85 yr. old) forest)
Shrubs:		
Pieris nitida	385	244
Smilax laurifolia	51	26
Leucothoë racemosa	43	0
Vaccinium corymbosum	42	4
Zenobia cassinefolia	29	0
Smilax walteri	19	4
Clethra alnifolia	0	10
Trees:		
Chamaecyparis thyoides	25	17*
Persea pubescens	0	98
Cyrilla racemiflora	0	40
Magnolia virginiana	0	20
Ilex myrtifolia †	0	20
Pinus taeda	0	18

* 70 per cent dead.

† *Ilex myrtifolia* is the only species not abundant in the vicinity of the middle-aged forest.

shrubs present, *Pieris nitida* (Bartr.) Benth. & Hook. was by far the most abundant, with 385 individual stems on the ten plots. This species was distributed evenly, being abundant on all plots. Other species were not only less abundant but also relatively infrequent. *Smilax laurifolia* occurred in six plots, *Vaccinium corymbosum* in five plots, while all others were found in less than 5 (one-half) of the plots. *Zenobia cassinefolia* and *Ilex lucida* (Ait.) T. and G. occurred principally under openings of the tree canopy. Both species are characteristic of open rather than forested bogs.

(*d*) *Cutover Portion of Young-Mature Forest and Shrub-bog Area*

In an area that had been cut over the shrubs which were present and rather dense in the forest had been released from competition. Opening the forest, and thus increasing the light, produces amazing results. Shrubs and vines grow into dense impenetrable thickets. Trees left by the loggers frequently may be overrun completely by the vines (figure 4). Seedlings of the cedar were scattered along paths or even were abundant where centers of logging activity, such as loading points, created local clearings in which excessive trampling killed back the shrub growth. Elsewhere seedlings were absent or extremely scattered. Dense shrubbery and vines evidently exclude cedar reproduction or at least greatly retard it.

Extensive areas of peat bearing a dense growth of shrubs and vines are very common on the southern coastal plain. Wells ('28) has described this shrub-bog or pocosin as it occurs in eastern North Carolina. Sometimes these border white cedar forests. Such is the case at Suggs' Pond where the shrub growth is tall and extremely dense. The southern white cedar does not invade it. Cedar seedlings were absent under the shrubs wherever the shrub-bog was examined. Perhaps this may be explained by the low light intensity. Light measurements taken near the surface of the ground under the shrubs in the well-developed pocosin area at Suggs' Pond were 3.8 per cent of full sunlight.

(*e*) *Mature Forest*

The trees of this 80-year-old cedar forest have tall, clear, straight trunks and small, high crowns. Scattered small, suppressed cedars are of the same age as the unsuppressed dominants. The dense understory consists of young bay trees and large pocosin shrubs. To the conspicuous tangle of smilax and small shrubs is added the confusion of occasional fallen trees.

The ground is very uneven. Large hummocks at the bases of the trees are interspersed with broad, deep depressions. The upper two feet of soil which has the reddish color characteristic of cedar peat contains only slight evidence of fire. At a depth of 2–3 feet, the peat is dark brown but contains only scattered charcoal fragments. Abundant charcoal below this level indicates severe and frequent fires at an earlier date. The total depth of peat is 8 feet with sand at the bottom.

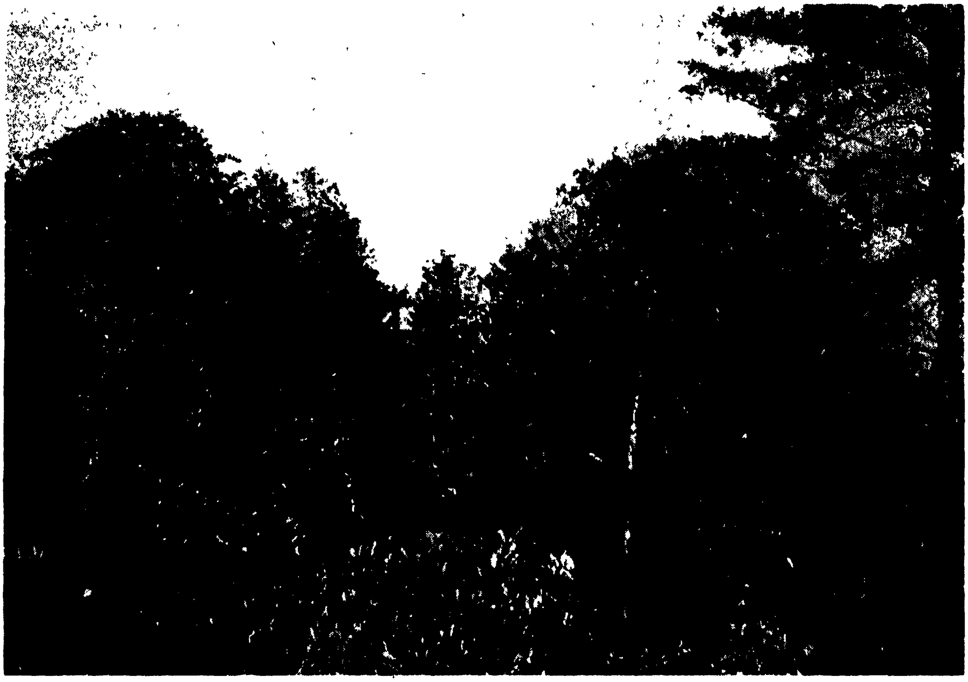

FIG. 4. Cutover area. *Smilax laurifolia* vines have overgrown small cedar trees forming dome-shaped masses over their crowns.

Light readings in this forest indicate somewhat greater light penetration (3.1 per cent of full intensity) than in the middle-aged forest. Readings in full shade were also higher (1.9 per cent).

Details of the composition of the forest as determined by the plot studies are indicated in table Ib. Southern white cedar averaged 17 individuals per plot. Seventy per cent of these cedars were dead. Five other tree species occurred. Of these *Pinus taeda,* with an average of 18 individuals per plot, was the only one that contributed to the forest canopy. The others were understory trees. The pines were either suppressed trees of the same age as the cedars, or older than the cedars, towering above them. One of the largest trees encountered was a loblolly pine 23.5 inches in diameter and 99 years old.

The other arborescent species were broadleaf evergreen or semi-evergreen bog trees. *Persea pubescens* (Pursh) Sarg., the swamp bay, was by far the most abundant. It averaged 98 individuals per 100 square meters. Following it in order of abundance were *Cyrilla racemiflora* L., *Magnolia virginiana* L., and *Ilex myrtifolia* Walt. with 40, 20 and 20 individuals per 100 square meters respectively.

No cedar or pine seedlings were found. Of the hardwood trees, *Magnolia virginiana* alone was absent in the seedling class. *Persea pubescens* represented 90 per cent of all the seedlings present, with a mere scattering of *Ilex myrtifolia* and *Cyrilla racemiflora.*

Among the shrubs represented, *Pieris nitida* was by far the most abundant with 244 stems per 100 square meters. *Smilax laurifolia* was second with 26 stems per 100 square meters. *Vaccinium corymbosum, Smilax walteri* Pursh and *Clethra alnifolia* L. were present but not abundant.

It was difficult or even practically impossible to make accurate ring counts of any of the broadleaf evergreen and semi-evergreen bog trees. *Magnolia virginiana* was most satisfactory in this respect. Attempts to count rings of several individuals of this species indicated trees from 19 to 70 years old. In the older individuals the rings showed very slow growth corresponding to the period of rapid growth of the cedars but rapidly increasing in growth rate about 15 years ago when cedar growth slowed down. An attempted ring count of some of the larger individuals of *Persea pubescens* and *Cyrilla racemiflora*, though the results are decidedly unreliable, did indicate that these were approximately 18–20 years old. *Ilex myrtifolia* wood is too uniform to allow even an unreliable count.

Discussion

The study of both the seedling stage of the forest as well as of reproduction in a logged-over area shows that the initiation of a southern white cedar forest requires an open seed bed on exposed peat soil. Peat soils in the southeastern coastal plain normally are clothed with a luxuriant ligneous vegetation of trees or shrubs, in eastern North Carolina more commonly shrubs. Even bog formation about lakes occurs only by an invasion of woody plants, there being no open sedge mat as about northern bog lakes (Buell, '39). Where such heavily vegetated peat soils are the usual thing, its requirement of an open seed bed makes the cedar community dependent for its origin upon some natural clearing agent. Certainly the sudden recession of impounded waters, such as exposed the seed bed referred to in the present study, could occur rarely under natural conditions. Fire seems the most likely clearing agent. But, as pointed out by Korstian and mentioned earlier in this paper, such a fire must occur at a time of high water table when the seeds in the upper layer of peat would not be burned. Controlled burning, as already mentioned, has been suggested as a silvicultural method for obtaining satisfactory regeneration of cedar.

That the cedar does not develop under the shade of other ligneous bog vegetation is shown by the data of the bog forests and studies of areas of pocosin shrub. There is a complete absence of white cedar seedlings in the cedar forest. The same is true of the well-developed pocosin shrub. Cedars possibly may start in the early, more open stage in development of the pocosin shrub, but rapid development of the shrubs and vines precludes their satisfactory establishment. Indeed, it was recognized by Korstian and Brush ('31) that while cedar seedlings sometimes may start under shrubs, usually the shade is so dense as to hinder or prevent seedling establishment. Under well-developed bog shrubs the shade is 3.8 per cent of full light intensity.

The question of natural regeneration after logging as mentioned above has been examined by Korstian ('24). It is especially significant that seedlings are limited principally to places completely opened up, where the full sunlight strikes the ground. Such places are rollways and tramways, and the extent of satisfactory regeneration is dependent upon the area of these and the degree of trampling in them. Where the slash is piled or the shrubs are not cut or trampled there is practically no cedar reproduction. When the cedar forest is opened up the already abundant shrubs and vines grow rapidly into exceedingly dense jungles. Smaller trees left by the loggers may be enveloped by massive growth of *Smilax laurifolia* and, to a lesser extent, *S. walteri* forming enormous green domes (figure 4). Isolated trees sometimes may have their tops completely broken off. It is small wonder, in such places where the vines are unmolested, that cedar trees, if they do start from seed, are rapidly overwhelmed.

Where the cedar seedlings start in mass on an extensive open bed they grow rapidly and successfully compete with the shrubs and vines which may start concurrently from seeds. Such a beginning results in a forest of closely-spaced, straight-stemmed trees. Wherever regeneration is more scattered, the trees suffer from competition with the shrubs. In certain parts of the middle-aged forest the trees are close together, and trunks are straight. In other parts of this forest the trees are more scattered and many of them have deformed trunks indicating severe competition in early development (figure 3).

A comparison of the middle-aged and mature forests, which represent an age span of 50 years, gives an indication of the probable normal trend in the development of the community as a whole. Certain details of the picture might be different had it been possible to study other comparable areas. Indeed the loblolly pines, the age of and older than the white cedars in the mature forest, are an element not present in the younger forest. However, in general, it is believed that a comparison of the composition of the vegetation of the two communities which were available reveals a reliable index of the trend to be expected in the maturation of the white cedar forest in this region.

If we consider the older forest in contrast to the middle-aged forest, there is a marked decrease in the number of shrubs and vines and an appearance of a number of broadleaf bog trees (table I). *Pieris nitida,* still by far the most abundant shrub, has decreased about 1/3 in abundance from the number in the middle-aged forest. Similarly, *Similax laurifolia* has decreased to one-half, *Vaccinium corymbosum* and *Smilax walteri,* respectively have been reduced to 1/10 and 1/5, while *Zenobia cassinefolia* and *Leucothoë racemosa* have disappeared entirely from the forest. On the other hand, the appearance of four species of broadleaf trees is conspicuous. *Persea pubescens* is by far the most abundant, being more than twice as abundant as *Cyrilla racemiflora* which is second in order of abundance. *Magnolia virginiana* and *Ilex myrtifolia* are present though scattered.

It would be exceedingly valuable to know the correct age of the hardwood species. However, except in the case of *Magnolia virginiana* it was not possible to make an exact determination. In *Cyrilla racemiflora* and *Persea pubescens* the rings are faint and indefinite and they are absent in *Ilex myrtifolia.* In the older individuals of *Magnolia virginiana,* which were close to 70 years, a rapid growth rate occurred during the last fifteen to twenty years. This corresponds to the period of slow growth of the cedars and possibly corresponds to a thinning of the canopy due to the maturation of the cedar trees. The larger trees of *Persea pubescens* and *Cyrilla racemiflora* were determined as about 18 years old. If the determination of the age of these is approximately correct the introduction of these species occurred at about the time the magnolias began their rapid growth or in other words when the cedars showed a definite decrease in growth rate. It is noticeable that there are occasional individuals of *Magnolia virginiana* practically as old as the cedars themselves. *Magnolia virginiana* is not wholly analogous ecologically to these other broadleaf tree species; in the first place it is only semi-evergreen, most of the leaves falling by mid-winter, and secondly, of these associated broad-leaved species *Magnolia virginiana* alone is absent in the seedling class. Light penetration of the cedar forest canopy does increase with the maturation of the community. Photometer readings in the middle-aged and mature forest showed a significant difference in light penetration of the canopy of the two forests. It is probable that the most marked thinning of the canopy of the mature forest occurred at the time, about 15 to 20 years ago, when as indicated by the rings, the growth rate of the cedars slowed up. That the advent of the understory broadleaf trees occurred concurrently with the increase of light penetration seems likely. This is somewhat supported by counts of the rings of the hardwood stems.

Fire is very common in the bogs of southeastern North Carolina and the southern white cedar is very easily killed by it. The chances of a southern white cedar forest indefinitely escaping such a catastrophe are slight. However, were the cedars gradually to die off from age, the bog hardwoods are already established. There seems little question that the forest under question, barring fire, in the natural course of succession will give way to a "bay" forest overwhelmingly dominated by *Persea pubescens* with the associated bog hardwoods *Magnolia virginiana, Cyrilla racemiflora* and *Ilex myrtifolia.* That this forest can perpetuate itself, with the probable exception of *Magnolia virginiana* which is absent in the seedling class, seems extremely likely. Ninety per cent of all seedlings present are those of *Persea pubescens* accompanied by a scattering of *Ilex myrtifolia* and *Cyrilla racemiflora.*

These results seem to indicate that on the coastal plain of southeastern North Carolina, in the natural course of succession, southern white cedar where it occurs on deep peat underlain by sand gives way to a bog climax of broad-leaved trees of which *Persea pubescens* is by far the most abundant but with which are associated 2 or 3 other species.

SUMMARY

Southern white cedar in southeastern North Carolina is a pioneer forest community on open peat soils. Its requirement of an open peat soil as a seed bed in an area where peat soils normally are clothed with a luxuriant woody vegetation makes cedar, as far as its origin is concerned, ordinarily dependent upon fire, the only natural clearing agent. To be effective this fire must occur only at a time of high water table when the raw surface peat containing the seeds cannot be destroyed. Once the cedar forest is initiated it becomes highly susceptible to fire. But if protected from fire the southern white cedar forest will give way in the natural course of succession to the bog climax, a broadleaf forest of swamp bay (*Persea pubescens*) with which are associated several other small evergreen or semi-evergreen hardwood species.

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EXPERIMENTS ON TOLERATION OF HIGH TEMPERATURE IN LIZARDS WITH REFERENCE TO ADAPTIVE COLORATION

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In 1939 the writer accumulated data bearing upon the relations of desert lizards to environmental conditions of radiant energy and high temperature.[1] These data were analyzed with respect to what the writer considered a well-established and fairly obvious principle of animal ecology, namely: that animals might, through natural selection, become adapted in their coloration to the physical conditions of the environment. Recently, stimulated largely by the publication of Cott's "Adaptive Coloration in Animals" (Cott, '39), there has been a revival of interest in animal coloration, in which the relationship of coloration to climatic conditions has been largely overlooked.

Despite the fact that Punnett ('15), Dobzhansky ('37), Shull ('36, '37), Hovanitz ('40) and others have called attention to the overemphasis frequently placed upon "protective coloration," the effect of Cott's book, whether intentional or not, has been to deny that the colors observed in animals may be adjusted to the physico-chemical environment. The current tendency seems to be to accept as habitat-adaptations only those cases where the coloration of the individual is directly induced by environmental conditions. In this category might be included those mammals which adopt a white winter coat as a direct response to reduced temperature. Other cases of environmentally induced coloration such as the classical cases described by Poulton ('87) of the effects of colored light on Lepidopterous larvae and pupae are generally described as adaptations entirely to predation factors.

The generalization that all animal colors are selected through the action of biotic factors in the environment, invariably leading to concealing colors, warning colors, mating colors, or mimetic colors, seems to be unwarranted. With other characters such as size and body-form which are common to all animals one finds examples of adaptations to the biotic component of the environment, to the physico-chemical component of the environment, and to the environment as a whole. In addition, animal characters may be non-adaptive. They may be of little or no significance to the survival of the species and yet be retained as accidental results of a gene combination which is otherwise advantageous. Conceivably, characters with some negative survival value may be retained if other advantages of the gene combination producing them outweigh the disadvantages. This phenomenon may give rise to othogenetic effects and result in the striking manifestations of degenerative evolution when the selection pressure in favor of a certain gene combination is relieved. There is no obvious reason why animal coloration should be selected in a manner different from other animal characters and much evidence can be brought forth to indicate that many color patterns serve a very specialized function in regulating the body temperatures of animals and in protecting them from harmful radiant energy.

It is the purpose of this article first to present some new data on the limiting high temperatures for desert lizards and on the environmental conditions which induce high body temperatures and second to review some of the evidence for the adaptation of animal coloration to physical conditions.

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[1] M. S. Thesis. University of Utah, 1939. Research sponsored by Dr. A. M. Woodbury.

EXPERIMENTAL MATERIALS AND METHODS

In these experiments a total of 128 lizards belonging to ten species and six genera were exposed to controlled conditions of temperature, radiation, and humidity under conditions which made it possible to determine the body temperatures of the animals throughout the course of the experiment. Table I lists the species used together with a brief statement on the ecology of each form. With the exception of the 16 *Scleroporus undulatus* which were obtained from Florida all of the lizards were captured in Northern Arizona and Southern Utah. All individuals were apparently healthy and would feed in captivity. The lizards were all catalogued with respect to size, sex, and length of time in captivity but, since none of these data correlates with experimental results, they are not presented here.

The experiments were for the most part run in a chamber constructed from a glass aquarium 9 in. by 9 in. by 13 in. One glass end of the aquarium was replaced by a wooden end through which holes were drilled to permit forced ventilation of the chamber and the introduction of thermocouples for temperature measurement. The holes were closed with corks when not in use. The bottom of the chamber was of sheet iron over which was placed a one-inch thickness of sand. Beneath the chamber was a 200-watt electric heating element connected to the 110-volt line through a rheostat which permitted regulation of the rate of heating of the sand. This heating element was so constructed that it heated the sand in all parts of the chamber very uniformly. A porcelain tube led through one of the holes in the end of the chamber and about this was wrapped a 600-watt heating element which could also be controlled by means of a rheostat. An electric fan at some distance from the chamber forced air through a flexible tube and the porcelain tube into the chamber permitting control of the air temperature without directly heating the chamber or the substratum. In most cases the chamber was loosely covered with a glass plate although in some experiments this glass was replaced with cellophane and the lizards were heated by radiation from a 450-watt quartz mercury-vapor lamp or by heat from a heating coil suspended above the chamber.

With this arrangement it was possible

TABLE I. *Summary of the natural history of the lizards used in these experiments.* ("Semi-desert" refers to pinon-juniper association, "Transition zone" to higher regions of pines and firs, and "Canadian zone" to Engelmann spruce association.)

Species	Habitat	Niche	Color
Sceloporus undulatus (Latreille)	Eastern pineland	Semi-arboreal	Darkest form. Blue-black
Sceloporus g. graciosus (Baird and Girard)	Transition to Canadian zone	Ground-dwelling	Variable gray. Light to dark
Sceloporus elongatus Stejneger	Semi-desert	Semi-arboreal	Dark gray
Sceloporus magister Hallowell	Semi-desert	Largely arboreal	Very dark gray
Uta s. stansburiana Baird and Girard	Semi-desert	Rock-dwelling	Light color. Red-brown
Sauromalus obesus (Baird)	Desert	Rock-dwelling	Very dark gray
Crotaphytus collaris baileyi (Stejneger)	Semi-desert	Rock-dwelling	Metachromatic
Phrynosoma douglassii ornatissimum (Girard)	Semi-desert to Transition	Ground-dwelling	Metachromatic
Phrynosoma platyrhinos Girard	Desert	Ground-dwelling	Very light gray
Cnemidophorus t. tessellatus (Say)	Semi-desert to Transition	Thick brush	Medium dark. Red-brown

to vary substratum temperature, air temperature, and humidity largely independently of each other. Humidity was varied by changing the moisture content of the sand substratum and by introducing a wick saturated with water into the air stream entering the chamber. Although two of these factors could not be held constant while varying the third, sufficient control was possible so that in no two experiments did the factors under consideration vary in the same way and the effect of each factor could thus be evaluated.

Humidity was read by means of a small hair hygrometer accurate to within 5 per cent relative humidity hung within the experimental chamber. All temperatures were read by means of thermocouples. These couples were of three types, namely: nickel-copper alloy and iron, nickel and copper, and copper and constantin. Each couple was calibrated separately and the cold junctions were kept in contact with melting ice. The voltages were read on a low resistance potential galvanometer in series with a variable resistance which allowed adjustment of sensitivity. A double pole, five-throw switch permitted five thermocouples to be connected to the galvanometer at once and read in rapid succession.

Two and sometimes three thermocouples were buried in the sand immediately beneath the surface in different parts of the chamber to check the uniformity of heating. The air temperature was read by means of two thermocouples hung, one at a height of one inch above the sand and the other at a height of four inches for use in the event that the lizard should climb the wooden end of the chamber. These couples were provided with shades to cut off direct radiant energy which might be absorbed by the metal.

The body temperature of the lizard was read by means of a couple composed of very fine wires (nickel and copper). The "warm junction" was inserted in the anus of the lizard and the lead wires were bent so that the couple could be held in place by a thread tied just anterior to the hind legs of the lizard. These couples did not interfere with free movements of the animals and in no apparent way did they alter normal behavior.

Temperatures read by the above means were always accurate to within 0.5° C. under the most unfavorable conditions. However, varying postures and behavior of the lizards considerably reduced the accuracy of the anal-temperature measurements.

A typical experiment usually required about 130 minutes during which time the temperature of the lizard was raised by one means or another from room temperature to a point where a fatal heat rigor was produced in the animal.[2] This end point was quite sharp and rather easily determined. As the body temperature approached the critical temperature the lizard would show symptoms of violent agitation, gasping and sometimes sporadic fits of burrowing and climbing. Finally convulsions occurred during which the lizard would, in some cases lie on its back and kick for several seconds and then right itself. The final temperature was indicated by violent tremors in various parts of the body (eyes, mouth, legs) and by a sudden paralysis of the hind legs. Cowles ('42) calls this the critical temperature for locomotory discoordination and finds an analogous reaction occurring in snakes at somewhat lower temperatures and Mosauer ('36) has suggested that these effects are due to the action of the excessive temperature on the cerebellar centers of equilibrium and muscular coordination. After the appearance of the paralysis the lizard usually died in from one to six hours regardless of treatment. In a few cases death did not occur for twelve hours and in four cases there was complete recovery within four hours.

Three of the specimens which recovered were of the species *Sceloporus undulatus*

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[2] As a behavior note it is interesting that the lizards move toward shade from the electric room lights when the body temperature nears the critical point.

TABLE II. *Summary of the lethal high temperature values obtained for 128 lizards of ten species*

Species	Number tested	Mean lethal temp. and S. E.	Range of lethal temperatures
Sceloporus undulatus	16	43.74 ± 2.03	40.3–49.0
Sceloporus graciosus	39	43.62 ± 0.42	39.5–50.0
Sceloporus elongatus	3	41.7	40.5–43.0
Sceloporus magister	7	43.0	42.0–44.6
Uta stansburiana	52	48.38 ± 0.26	45.5–51.0
Sauromalus obesus	2	42.7	39.0–46.5
Crotaphytus collaris	3	46.5	45.0–47.5
Phrynosoma douglassii	3	45.5	44.0–47.0
Phrynosoma platyrhinos	2	45.5	45.0–46.0
Cnemidophorus tessellatus	1	46.0	
TOTAL	128	45.6	39.0–51.0

and the fourth was a *Phrynosoma douglassii.* One *undulatus,* after recovery, was again heated until paralysis occurred and made a second recovery. This lizard failed to recover from the third experiment. Since the animal was given no chance to replenish lost body water between trials it is possible that death in the third experiment may have been due to desiccation. In all three tests the paralysis appeared at approximately 42° C. The only other lizard in which a second paralysis was produced was the *Phrynosoma* and this specimen failed to survive the second trial.

EXPERIMENTAL RESULTS

The data on the extreme high temperatures tolerated by each species are presented in table II. Only three species are represented in sufficient numbers, in view of the variability of the results, to permit the drawing of even tentative conclusions from these data.

As an *a priori* assumption it would be logical to expect lizards of different habitats to show different degrees of toleration to high temperatures. However, Mosauer ('36) failed to find any such differences. As he says: "Contrary to popular belief, the toleration of excessive temperatures by desert reptiles is no greater than could be expected of poikilothermous reptiles and no greater than that shown by nocturnal snakes." It is of interest to note (table II) that the average value of the lethal temperature obtained from these experiments (45.6° C.) [8] is lower than the lethal temperature (46.8° C.) postulated as the upper limit for birds (Baldwin and Kendeigh, '32). This conflicts strongly with the popular belief that reptiles are anmals particularly immune to injury from the sun's rays.

Mosauer and Lazier ('33) have concluded that death from insolation in reptiles is due entirely to overheating and not to any actinic role played by the radiation. In this series of experiments 104 lizards received their lethal temperatures via conduction from the substratum while the other 24 were heated by the direct absorption of radiant energy. In those killed by conduction the average lethal temperature was 45.5° C. while in those killed by radiation the average lethal temperature was 45.8° C. These results are extremely close together, considering the wide range of values obtained, and thus these data support Mosauer's conclusion entirely.

If death from insolation is dependent only upon the maximum temperature attained the limiting temperature should show no correlation with the rate of heating. Previous experimental results (Dallinger, '87; Davenport and Castle, '95; Jollos, '21) have indicated that in some animals (flagellates and tadpoles) the toleration temperature may be raised by keeping the forms in constantly high temperature. The deleterious effects of high temperature on the body are largely the result of chemical reactions in the protoplasm while the deleterious effects of low temperatures are largely mechanical, involving the water of the tissues. At low temperatures animals have an increased capacity for water-binding so it would not be surprising to find that cooling influences the minimum toleration temperature more than heating influences the maximum toleration temperature. On the other hand, rapid temperature changes have a powerful stimulating effect on the organism and may affect the melting point of lipids in the body (Heilbrunn, '38) and one might accordingly anticipate some slow acclimatization to high temperatures.

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[8] By coincidence Cowles ('42) gives the value 45.6° C. as the critical maximum for lizards. He finds the analogous temperature for snakes to be 39.1° C.

No attempts at acclimatization were made in these experiments but the rate of heating varied widely between trials. Fig. 1 is a scatter-diagram showing the rate of temperature increase plotted against the maximum temperature attained for 22 trials in which the rate of heating was essentially constant throughout the trial. It clearly indicates the lack of correlation between the rate of temperature increase and ability to withstand high temperatures. This means that the lizards cannot, in these brief time periods, become adjusted to higher temperatures.

Fig. 1 suggests confirmation of Mosauer's conclusion that death from high temperatures in reptiles does not result from desiccation produced through the evaporation of body fluids for, if desiccation were playing a part, one would expect those lizards which were heated most rapidly to survive the highest temperatures.

The ability of amphibians and mammals to endure high atmospheric temperature is, of course, intimately related to their ability to lose body heat through evaporation of

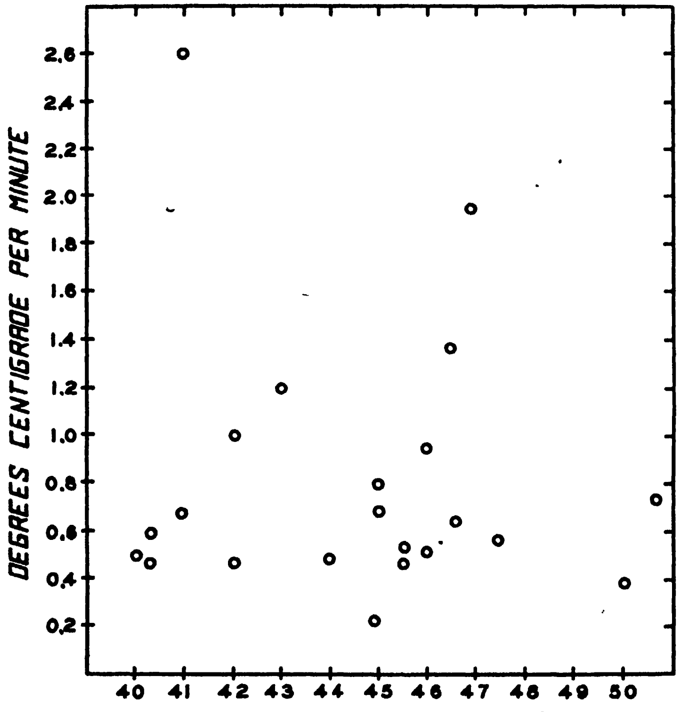

FIG. 1. Absence of correlation between rate of temperature increase and maximum temperature tolerated by 22 lizards in experiments in which the rate of heating was constant.

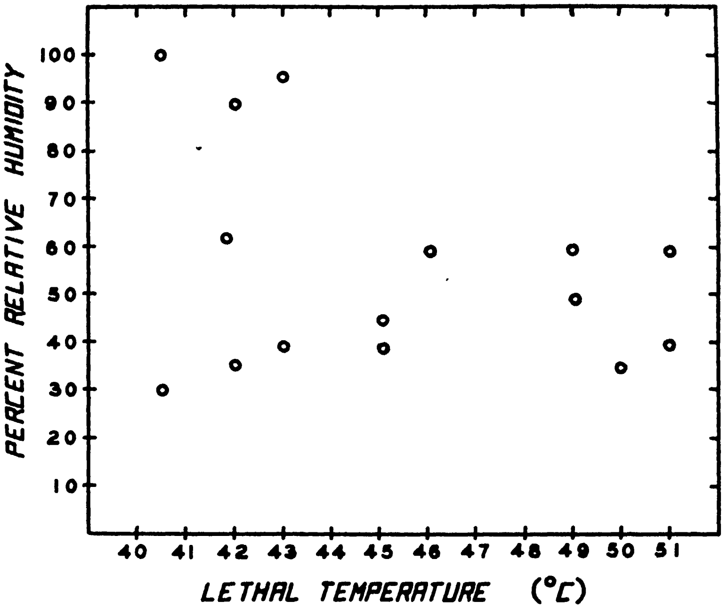

FIG. 2. Absence of significant correlation between relative humidity and lethal temperature for 15 lizards.

water. This ability depends directly upon the evaporating power of the air.[4] When lizards get excessively warm they always open their mouths and "pant" which permits the evaporation of moisture from the lungs and is effective in cooling the animals. Lueth ('41) and Cowles ('42) both found that at high temperatures the body temperatures of snakes might remain below that of their surroundings. In these experiments, when the means by which two lizards were heated were comparable, the lizard in the higher humidity always showed a more rapid rise in body temperature. Table III illustrates this effect for two adult male *Sceloporus undulatus* similar in size and coloration heated simultaneously by the mercury-vapor lamp but in separate chambers and exposed to different conditions of relative humidity.

These results show that even in desert reptiles evaporation may permit the animals to make short excursions into conditions of high temperature which they could not endure for long periods. It seems very probable, however, that desert animals cannot afford to use water for thermoregulation except under emergency conditions.

While evaporation of moisture enables a lizard to endure excessive environmental temperatures for longer periods of time it does not seem to affect the maximum body temperature which the lizard can survive. Fig. 2 is a scatter-

TABLE III. *The effect of relative humidity on survival time in two lizards tested simultaneously*

Species	Relative humidity	Lethal temp.	Time to reach lethal temp.
Sceloporus undulatus	100%	40.5° C.	4.5 minutes
Sceloporus undulatus	30%	40.5° C.	26.0 minutes

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[4] The evaporating power of the air is a function not only of the relative humidity but also of the air movement. Thus humid air which is in rapid motion may, in certain habitats, be more effective in cooling an animal than is dry quiet air. This point is frequently overlooked as when an animal's cooling mechanism is assumed to be ineffective in the humid air of a beach habitat.

diagram in which the constant relative humidity for 15 trials is plotted against the lethal temperature. It indicates the total lack of correlation between these two factors.

SPECIES DIFFERENCES

As mentioned above the lizards used in these experiments showed no special abilities to endure high body temperatures which would distinguish them from other groups of vertebrates. The results likewise fail to indicate that the species which, by virtue of their adjustment to special habitats, would apparently be most benefited by such abilities are exceptional in this respect although many of the species are represented by too few individuals to permit definite conclusions. *Sauromalus obesus* and *Phrynosoma platyrhinos,* the two genuinely "hot climate" species used, are quite average in the temperatures endured. However, the difference in average lethal temperature between *Uta stansburiana* and either *Sceloporus undulatus* or *Sceloporus graciosus* is statistically significant. In general, *stansburiana* inhabits hotter regions than either of these other species and this difference in temperature toleration may represent an actual adaptation to life on the hot desert. If, as has often been suggested (Pearse '26, Heilbrunn '38), heat rigor is the result of protein decomposition, adaptive differences of this type may prove of considerable interest. It should be pointed out, however, that *Uta stansburiana* is a considerably smaller form than any of the others used and that some constant experimental error may have influenced these results. For instance, the thermocouple may not have penetrated so deeply into the smaller anal opening of the smaller species or the rectal temperature might be different from the temperature of the body in general. Actually, purely qualitative tests have given some indication that the anal temperature is not always the same as temperatures taken by mouth. No oral temperatures were taken in these experiments as it was desired to permit the animals all possible freedom of movement. The great range of differences in temperature toleration observed between individuals, as indicated by table I is probably explicable on the basis of experimental errors. In view of this difficulty, conclusions based on data of this type are unreliable unless analyzed statistically.

THE MEANS BY WHICH THE LIZARD BODY ACQUIRES HIGH TEMPERATURES

The body temperature of a lizard under natural conditions may be raised in four principal ways as follows: (1) by conduction from the air, (2) by conduction from the substratum, (3) by metabolism and muscular activity, and (4) by the direct absorption of radiant energy. The methods employed in these experiments provide a ready means of evaluating these four sources of temperature and hence give an indication of the heating and cooling influences to which lizards are subject in nature. A graph was made of each individual experiment showing the variations in soil temperature, air temperature, body temperature, and relative humidity. Such graphs clearly indicate the relation between body temperature and these other factors. If the substratum was not heated from below but heated air was blown into the chamber the lizard's temperature would, in no case, rise more rapidly than the temperature of the sand. If, on the other hand, the substratum was heated while cold air was circulated through the chamber the body temperature of the lizard still followed the temperature of the substratum. The cold air reduced the rate of temperature increase of both the lizard and the sand but the body temperature readily rose to the lethal level even when exposed to air at a temperature 15° C. below this level. Air temperature is thus of minor importance in regulating the body temperatures of lizards. In nature, if a lizard can find a substratum at an endurable temperature, air temperature will not be effective in producing overheating. These data suggest that too much importance has often been attributed to air temperature in this connection. Leuth ('41) considers that air temperature and radiation are the most effective factors in determining the body temperatures of snakes.

In desert regions the substratum temperature during the day usually runs much higher than does the air temperature. Records of such temperatures are to be found in Buxton ('23) and Mosauer ('36). Briefly, air temperature very seldom exceeds 45° C. while rock and sand temperatures frequently run as high as 65° C. Cowles ('39) reports a substratum temperature of 87° C. Rock and sand, however, are poor heat conductors so that the temperature may decrease by 15° C. in the top 5 cm. and 26° C. in the upper 10 cm. (Hesse, '37). The burrowing habit is thus an effective adaptation for avoiding excessive temperatures. At night the desert soil cools very rapidly due to its low specific heat and thus provides favorable conditions for crepuscular and nocturnal activity during the hotter parts of the year.

Small body size resulting in a greater surface-mass ratio may greatly simplify the problem of temperature control in lizards. Cowles ('41) has concluded that small size enables some reptiles to remain active for a longer part of the year as they are better able to attain optimum temperatures during the short warm periods of spring and fall days. He further suggests that small size may lead to overheating in midsummer. However, since we have found that air temperature is not effective in raising lizard body temperatures, we might anticipate that small body size would also be advantageous in very hot weather and this actually appears to be the case. When individuals of *Uta stansburiana* (our smallest species) are heated simultaneously with individuals of *Sceloporus undulatus* (a larger and much darker-colored form) by means of conduction from the substratum, the *Utas* are always slower to take on excessively high temperatures. Apparently in this case the smaller size of the *Uta* more than offsets the advantage of the darker color of the *Sceloporus*.

Metabolism and muscular activity are effective only to a very slight extent in raising the temperature of a lizard. In these experiments the excitement caused by inserting the rectal thermocouple before beginning each experiment usually raised the body temperature by about 2° C. After periods of violent activity the temperature would sometimes be raised by from 0.5° C. to 1.5° C. but the increase was always so slight that it could contribute little or nothing toward raising the animal's temperature to the toleration limit. Leuth ('41) obtained similar results with snakes. Handling of some lizards such as *Anolis* commonly induces change to the light color phase, a character usually associated with increased body temperature.

In those experiments where the lizards were heated by infra-red radiation from above, the sand temperature always rose more rapidly than did the body temperature so it was impossible to determine whether heating of the animal was from the substratum or from the radiation directly. However, when the mercury-vapor lamp was directed into the chamber the body temperatures of the lizards rose more rapidly than did the sand temperature. This must mean that, at the shorter wavelengths, the absorption by the skin of the lizards is very much greater than the absorption by the sand since the specific heat of protoplasm is much higher than that of sand. Other tests have shown that the intense desert sunlight will also raise a lizard's body temperature at least as rapidly as it will raise the temperature of a light-colored sand substratum. It has been estimated (Krüger and Kern, '24) that lizard skin absorbs close to 80 per cent of the incident radiation. Insolation then must be extremely important in nature in raising the body temperatures of lizards.

The importance of this source of heat will, of course, vary with the color of the

TABLE IV. *Species differences in rate of heating correlated with coloration.* (Animals exposed to light of mercury-vapor lamp)

Species	Color	Relative size	Temperature rise after 26 minutes
Uta stansburiana	Light red-brown	Smallest	11° C.
Sceloporus graciosus	Dark gray	Intermediate	13° C.
Sceloporus undulatus	Dark blue-black	Largest	14.5° C.

lizard as darker pigments absorb a greater amount of radiant energy. When individuals of several species of lizards were exposed to the mercury-vapor light the rate of temperature increase was directly proportional to the darkness of coloration of the animals. Table IV illustrates this point for three lizards tested simultaneously in the same chamber.

It has long been observed that the coloration of certain reptiles varies with the temperature of the body. In general, the tendency is towards lighter colors at higher temperatures. The important researches of Atsatt ('39) have shown that this tendency is much more general among the desert lizards of Southern California than had formerly been supposed. Her results also show a number of good correlations between color-phase and the need for absorption or emission of radiation. Most of the species with which she worked were in the light color phase at high temperatures and in the dark phase at low temperatures. Such a color change could obviously aid a lizard in reaching an optimum body temperature by absorption of radiant energy and then reduce further absorption to lessen the danger of overheating. In other species an additional factor is involved so that, at moderate temperatures, the presence of illumination induces the dark phase while absence of illumination induces the light phase. Such a mechanism might enable the animal to reach an optimum temperature earlier in the morning and conserve body heat later into the evening. Cowles ('41) has suggested that the light colors of nocturnal desert reptiles may aid the conservation of body heat and he has stated ('39) that the lack of a capacity for color change in snakes is important in restricting many forms to nocturnal, crepuscular, or subterranean activity. Atsatt found that the nocturnal lizards of the genus *Xantusia* always assume the light color phase in the late afternoon and evening apparently regardless of light and temperature conditions. Perhaps the most significant of Atsatt's findings was the discovery that the temperature necessary to induce the color change for each species was related to its habitat. "The high temperature which is critical for change from the dark phase to the light phase is lower in *Phrynosoma b. blainvillii,* a valley form, than in *Phrynosoma platyrhinos,* a desert form. *Uta stansburiana stejnegeri,* the only lizard active on cool days and cool mornings in the desert, has its critical temperature at 25° C. instead of 35°–43° C." (the range characteristic of most of the species tested by Atsatt).

Parker ('34) has attempted to relate the presence of racial melanism among lizards in certain localities to climatic conditions; and Klauber ('39) has made a similar attempt although he has criticized some of Parker's assumptions as to the habits of the lizards in question. Klauber appreciates that many of the described cases of animal coloration are explicable either as concealing coloration or as adaptations to climatic conditions. For the reptiles of the Southwestern United States he has concluded that, in cases where these two ends to be served by coloration run counter to each other, dominance has been assumed by the concealing colors. Atsatt's results as well as the results discussed above suggest that coloration may serve a very real function in controlling body temperature.

Except in very humid regions the ability of animals to lose heat by evaporation of water permits some measure of control over body temperature irrespective of coloration. The frequently observed relationship between high humidity and dark coloration strongly suggested that when cooling by evaporation is restricted a selection value is assumed by colors which will radiate heat rapidly.

Under desert conditions there are a number of ways in which a species might moderate the deleterious effects of an unfavorable coloration. The burrowing habit, hibernation, nocturnal activity, and reduced body size might compensate to some extent for either undue conspicuousness or excessive absorption of radiant energy. It is only in cases where the needs for concealment conflict with the needs for temperature control that we can correlate observed animal colors with either factor alone and most of the described cases of adaptive coloration are not of this type. It is a much neglected point that most cases of concealing coloration are also subject to an alternative explanation. Another frequently overlooked point is that climatic conditions, in the majority of habitats, set rigid limits to the range of possible animal colors which can be adopted by a successful species.

THE FUNCTION OF LIGHT IN RESTRICTING ANIMAL COLORS

Because of the current tendency to overlook the relationships between animal colors and the physical environment some of the principles involved may be briefly surveyed here. Detailed discussions of the physics and physiology involved are to be found in Laurens ('33) and Duggar ('36).

The first point worthy of notice is that all animals commonly exposed to radiant energy must possess some filtering mechanism sufficient to shield the vital organs from any radiation which might penetrate and be absorbed by these organs with resulting heating effects or abnormal chemical reactions. Any penetrating radiation which is absorbed by the internal organs may produce deep heating of the tissues and photochemical reactions to an extent depending upon the intensity of the radiation, the amount absorbed by the tissues, and in inverse proportion to the wavelength of the radiant energy.

The vast majority of animals are never exposed to intense radiation and even among terrestrial animals the majority are nocturnal in habit. Of those which are exposed to sunlight the filtering requirements will vary with the chemical composition of the tissues which determines what radiation will be absorbed. These requirements are best understood in the case of vertebrates which, due to the presence of hemoglobin, absorb radiation throughout most of the visible spectrum except in the red range. Translucent vertebrates are typically nocturnal like the gecko *Coleonyx* or subterranean forms such as *Rhineura.*

Bird feathers and the hair of mammals are effective in stopping the shorter wavelengths of solar light and melanin is a very effective general filter. Under conditions of intense light, wavelengths in the visible yellow range may penetrate deep within the bodies of vertebrates and increased pigmentation or reflecting surfaces may be required under these conditions.

The presence of pigmented tissues which protect the internal organs from radiant energy has been recognized in the literature for many years. Wallace ('87) stated that all tropical animals exposed to the sun have highly pigmented skins or very thick coverings of hair or feathers while the nocturnal forms may lack these traits. Watkins-Pitchford ('09) noted that ground-dwelling forms are more darkly pigmented on the dorsal parts, that lower vertebrates exposed to light have the peritoneum pigmented if the epidermis is unpigmented, that the peritoneum is black in some colorless fishes while it may be colorless in dark-colored forms, and that truly black beetles are inclined to be very light-colored internally. Krüger and Kern

('24) pointed out that sun-dwelling amphibians and reptiles invariably have the central nervous system and the gonads protected by pigmented tissues which are frequently absent in related nocturnal forms. Krüger ('29, '31) has actually demonstrated the effectiveness of the pigments of amphibians and reptiles as protective filters against long wavelength radiation. The pigmentation of the pia mater is said to be more abundant in brunette Europeans and brown Egyptians than in the black peoples such as the Sudan Negros (Hesse, '37). Klauber ('39) discussing coloration of the reptiles of the Southwestern United States, points out that there is a black body-lining in the lizard genera *Uma, Callisaurus, Crotaphytus,* and *Phrynosoma,* while it is absent from the nocturnal *Coleonyx* and from *Cnemidophorus* which is relatively a shade-dwelling form. In *Dipsosaurus* he found the belly wall to be shiny white outside and dead black inside. Particularly interesting were his observations on three species of the nocturnal genus *Xantusia* in which he found the black peritoneum present in two species and absent from one (*X. henshawi*). Strong ('03) found that white bird feathers transmit extremely little light. Woodruff ('15) suggested that a year-round thick coat of fur might serve as a light filter in forms such as the musk-ox, caribou, certain bears, and the Tibetan snow-leopard which have white skins. In all of these white-skinned forms the exposed lips and nose are heavily pigmented. Animals with thin fur such as the zebra, or which lose the thick fur in summer, as in the wild ass, tend to have black skins if they are exposed to the sun. Woodruff states that the same principle applies to domestic stock. The tanning process in man is believed to be important in shading the internal organs. Kalmus ('41) states that mosquito larvae (*Corethra*) living in deep water are colorless while surface forms tend to be dark colored and Vilter ('30) finds that intense sunlight increases the number of melanophores developed in amphibian larvae. In spite of these excellent correlations with physical conditions Cott concludes that, in the Tortugas fish *Coralliozetus cardonae* which has a transparent trunk musculature, the heavily pigmented peritoneum is present for the sake of counter-shading to make the animal less visible to predators.

A second great way in which pigment may be related to the physical environment of the animal is in connection with temperature control. As we have seen, when two animals are simultaneously exposed to intense radiant energy, the darker-colored animal will be subject to the greater heating effect. Conversely, if the animals can find shelter from the radiation, the dark colored animal will lose heat more rapidly providing it is at a higher temperature than its surroundings. For any animals that remain exposed to supra-optimal temperature conditions for any considerable time, dark colors must necessarily be a disadvantage. This will be particularly true in humid climates where cooling by evaporation is retarded or of animals which for any reason do not ordinarily lose heat by evaporation. The shift to lighter colors at high temperatures in desert reptiles is probably very important in this connection. Woodruff ('15) pointed out that dark-colored peoples have never established themselves in the very hottest regions of the earth and Seevers ('38) mentions that captive polar bears may withstand heat better than some tropical animals.

The light coloration of desert animals in general is explicable on this basis without resorting to a theory of biotic selection. On the other hand, there seems to be a tendency for rock-dwelling forms to be more darkly colored than those dwelling on light sand and Klauber concludes that in these cases the selection favoring concealment has taken precedence over the requirements for temperature control. Woodruff ('15) believes that a similar situation exists in the case of domestic animals where man has relieved the selection pressure favoring concealment and replaced it with a selection for better performance with the result that the colors of work animals come to be adapted to the physical environment. He states that black horses are preferred in hot cloudy climates with a high humidity while Arabian horses are adapted to conditions of intense illumination by the possession of light colored hair and a black skin.

Lewis ('42) has reviewed some of the widely scattered information relating to the functional aspects of the color differences existing between races of *Homo sapiens.* Good correlations exist between human pigmentation and the physical conditions of the environment while it would be extremely difficult to explain the observed differences on the basis of predator selection.

The relation of animal colors to temperature control may be obscured in many ways. The habits of animals may become adapted through burrowing, hibernation, or nocturnal activity to utilize coloration which might otherwise be unfavorable. Cooling by means of evaporation may sometimes be the primary means of temperature control.

Animal coloration, like other animal characters, may also appear as a purely indifferent (or apparently somewhat harmful) result of gene combinations which are selected for their effect on entirely different characters. Kalmus ('41, '41a) points out that the same processes are responsible for the hardening and darkening of insect cuticles. Consequently, insects which must resist mechanical abrasion or desiccation are likely to be dark in color even when, as on the desert, the color itself might not be the most favorable. The metallic colors of some insects may represent a compromise in this connection as they possess the hardness of dark cuticles and yet reflect much radiant energy due to their surface structure.

Hopkins ('95) finds that the white color of the wings of the cabbage butterfly *Pieris brassicae* is due to the storage of uric acid and Wigglesworth ('24) believes that the family Pieridae is unique in this respect. Conceivably such a mechanism could have arisen due to a selection pressure with respect to color but it is much easier to assume that the need for storage of metabolic wastes has prevailed and that the resulting color is an accidental by-product of this process.

One might expect that in arctic regions animal coloration would be most intimately related to physical conditions for animals can scarcely escape exposure to radiant energy during the long period of almost constant light. Cott finds many cases of coloration in arctic animals somewhat puzzling on the basis of biotic selection while most of these cases may be shown to correlate well with climatic conditions.

Animals living in cold bright climates must be protected from penetrating radiation but can ill-afford very dark, light-absorbing colors which would make for great loss of body heat whenever the animal was not exposed to light. In the arctic the best possible arrangement by which homoiotherms could meet these requirements would seem to be a seasonal color change in which the animal wears dark, light-absorbing colors during the long period of constant light and then adopts a light colored, heat-retaining coat during the period of cold and constant darkness. This arrangement would be particularly advantageous for smaller animals which, in accordance with Bergmann's principle, are more subject to heat loss than are the larger forms. The stoat, arctic fox, ptarmigan, and many other animals change color in this way.

Because some of the arctic animals which turn white in winter may do so without being exposed to temperature changes, Cott concludes that their colors must be adaptive (i.e. concealing). Actually the arctic fox, *Alopex,* which adopts a white winter coat in the northern part of its range but not in the less intense Icelandic winter would seem to be correlated more closely with light and temperature conditions than with requirements for concealment. Cott provides evidence that this rhythm is inherent rather than an individual response when he mentions that the arctic foxes in the London Zoological Gardens regularly turn white in winter. We may take it for granted that these individuals were not imported from Iceland.

If the animal possesses dark skin, is a sufficiently good reflector, or is otherwise protected against the penetration of radiation it may retain the white coat throughout the year as do the polar bear and the snowy owl. On the other hand, animals which remain dark colored throughout the year as do the musk-ox, raven, wolverine, sable, rabbit, and reindeer, while they are protected against penetrating radiation must be favored by very good heat insulation or through habits which will reduce heat loss during the arctic night. Shades of red, brown, or yellow which prevent light penetration but do not radiate heat as rapidly as black would theoretically be most advantageous for such animals.

In regions other than the arctic similar principles might be expected to operate but, as mentioned earlier, adaptive behavior may obscure the relationships.

Unquestionably, objections can be raised to the above generalizations if presented as the final explanation of the colors of arctic animals. However, these principles fit the facts at least as well as does the hypothesis of protective resemblance and are presented here, not as a final explanation of animal coloration, but to indicate that the notion of cryptic coloration selected entirely by biotic interrelations has been overworked on the basis of the known facts. On the other hand, the survival value of protective resemblance, no matter how such resemblance may have been acquired, has been demonstrated in a number of cases. The experiments of Jones ('32) and Isely ('38) are among those which demonstrate that predators may feed differentially on animals depending upon whether or not they resemble their surroundings. Other lines of indirect evidence also support the theory. The greater incidence of melanism in insular forms as opposed to mainland individuals (Mertens, '34) strongly suggests that predation pressure is a factor of importance.

The effects of predator selection in influencing the evolution of animal colors cannot be neglected but attempts to oversimplify the situation by neglecting physico-chemical factors and the role of accidental and incidental variation are likewise unjustified.

Just as with concealing coloration, many cases of "warning coloration" are susceptible to a much neglected alternative explanation. If an animal really is for some reason unsuitable for prey, any selection pressure favoring concealing colors should be relieved and unadaptive colors might be expected to appear as incidental results of new gene combinations. Cott believes that skunks and porcupines are "warningly colored" and yet neither of these forms would ordinarily be killed or injured in the process of "teaching" a predator that it is undesirable. While it is conceivable that such a mechanism might have grown up very gradually through a long phyletic process one must remember that any selection in favor of warning colors would have to act in spite of a predation pressure which would presumably be increased by conspicuousness. Skunks are subject to predation by owls while weasels, fishers, and wolverines are all known to eat porcupines.

SUMMARY

An experimental technique for studying the ecological effects of radiant energy and high temperatures on lizards is described. This technique permits temperature and humidity readings to be made at any time without disturbing the animals and permits separation of the factors of air temperature, substratum temperature, relative humidity, and body temperature.

The limiting high temperatures for 128 lizards of ten species were determined. The mean lethal temperature was 45.6° C. There is some indication that differences between species exist in the ability to en-

dure high temperatures and to recover from heat rigor. No differences are noted with respect to sex or length of time in captivity.

Mosauer's conclusion that death from insolation in desert reptiles is purely a thermic effect is verified and the lethal temperature is found to be independent of the rate of heating.

It was found that desert lizards can markedly control body temperature by the evaporation of moisture from the lungs.

Substratum temperature and incident radiation are important in raising body temperature while air temperature and muscular activity have very little effect.

Small body-size permits rapid cooling and is an advantage to desert reptiles.

Dark colored lizards are more readily overheated by the absorption of radiation than are light colored forms.

Some of the evidence for the adaptation of animal colors to physical conditions is discussed, with the conclusion that too much emphasis has been placed on concealing coloration .

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NOTES AND COMMENT

FURTHER EVIDENCE ON CHEMICAL FACTORS AFFECTING THE MIGRATORY MOVEMENTS OF FISHES, ESPECIALLY THE SALMON[1]

INTRODUCTION

The senior author has long believed that the response to a carbon dioxide tension gradient is a dominant factor in determining the migratory movements of the salmon. It should be needless to state that it is not his opinion that carbon dioxide tension is the sole factor but that it is a dominant factor in the spawning migratory movements from the marine feeding grounds to the spawning streams. Before this view can be accepted as a working hypothesis it must be shown:

(1) that salmon do respond to a carbon dioxide tension gradient in sea water;
(2) that there is a possibility of a carbon dioxide tension gradient from the spawning streams to the feeding grounds of the salmon;
(3) that fishes can respond to a very slight carbon dioxide tension gradient; and
(4) that fishes have receptors sensitive to the carbon dioxide tension of the water.

1. It has been shown (Shelford and Powers, '15, and Powers, '21) that salmon and other marine fishes do respond to a carbon dioxide tension gradient in sea water.

2. The possibility or the probability of a carbon dioxide tension gradient from the mouths of spawning streams to the salmon feeding grounds has been pointed out (Powers, '41).

The following experiments were undertaken to throw light on the other two points.

Salmon were not available to the authors hence the brook trout, *Salvelinus f. frontinalis* (Mitchell) and the rainbow trout, *Salmo gairdnerii iridus* Gibbons, the latter a close relative of the Pacific Coast steelhead, were selected as experimental fishes.

Acknowledgments.—First the authors wish to thank Mr. E. L. Green, Assistant Wildlife Technician, and Mr. J. R. Eakin, Superintendent, The Great Smoky Mountains National Park, for cooperating in making fishes available without which the experiments here reported could not have been carried out.

Methods.—The gradient tank technique developed by Shelford and his students (Shelford, '29) has been utilized in these experiments. The gradient tank, 126 cm long by 18 cm deep by 14 cm wide, employed was patterned after the tank described by Shelford ('18) and modified by having five outlets in center at the bottom and five on each side near the top, one at center and two equally spaced between the center and each end.

In order to more completely control the carbon dioxide tension of the water at the two ends of the gradient tank without modifying other factors, a thirty gallon, well aerated aquarium with an overflow and with an inlet only sufficiently great to form a relatively small outflow was used as a source of water supply. This insured a water supply with oxygen and carbon dioxide tensions approximately in equilibrium with atmospheric air partial pressures. A more important fact was that the water supplied to the two ends of the gradient tank was identical in physico-chemical characteristics except when modified. Water from the aerated aquarium was syphoned into a six liter by 48 cm high bottle above each end of the gradient tank to serve as heads to feed the two ends of the gradient tank. The flow at each end of the gradient tank was approximately 1500 ml per minute. Carbon dioxide was bubbled through the water of one of the feed bottles at the rate of four to eight bubbles per minute. This added very little carbon dioxide to and removed practically no oxygen from the water. This obviously would form a carbon dioxide tension gradient between the two ends of the gradient tank. However, except when carbon dioxide was bubbled into the bottle at a higher rate a gradient could not be detected by measuring the pH of the water at the two ends of the tank with a Beckman pH meter.

Experimental Data and Discussion.—A total of forty-one gradient tank experiments, twenty seven rainbow and fourteen brook trout, were run. Figures 1 to 3 are typical graphs of the first twenty minutes of experiments lasting over periods of from thirty to sixty minutes. Graph 5, figure 3, is an exception and will be described later. Graphs 1 to 4, figure 1, are of one and the same fish—a rainbow trout. Graph 1 shows a definite negative response to carbon dioxide tension between a tension approximately the same as the carbon dioxide partial pressure of atmospheric air and slightly above. Graph 2 is a control where the carbon dioxide tension is the same at the two ends of the gradient tank and approximating the carbon dioxide partial pressure of the air. No preference is shown by the fish for either end of the tank. To further test the ability of the two species of fishes to re-

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[1] Contribution no. 9, Department of Zoology and Entomology, University of Tennessee, Knoxville.

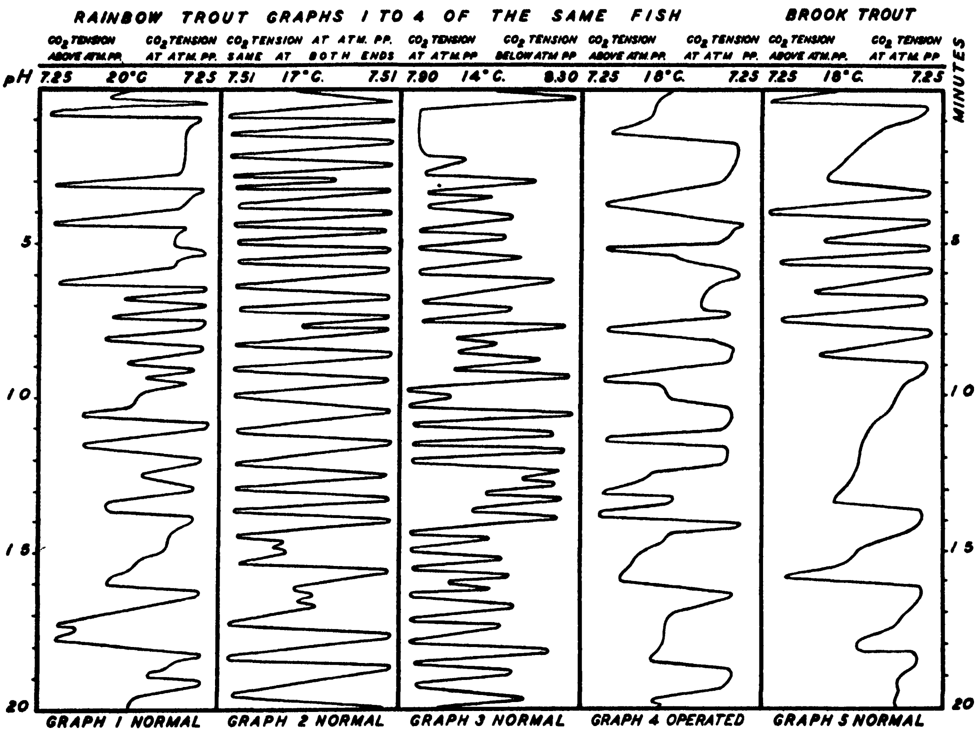

Fig. 1. Graphs 1 to 4 are of one and the same fish; graphs 1, 3, and 5, are carbon dioxide tension gradient experiments. No. 4 is a graph of responses of the rainbow trout in a carbon dioxide tension gradient after the nerves leading to the lateral lines were clipped. (This figure, along with 2 and 3, is a graphic representation of the movements of the fish in the gradient tank. Following the technique of Shelford (1929) in experiments the water entering one end of the gradient tank was modified while in controls the water entering the two ends was physicochemically identical. In all experiments the left side of the graph always represents a higher carbon dioxide tension than the right side. The time of the experiments and controls is indicated along the sides of the figures.)

spond to a carbon dioxide tension gradient, 1 N sodium hydroxide was added to the second feed bottle at the rate of four drops per minute after the carbon dioxide had been stopped bubbling through the first feed bottle. The fish showed a positive response to the higher carbon dioxide tension end of the gradient tank, graph 3, figure 1. That is, the fish responded positively to the carbon dioxide tension nearest the carbon dioxide partial pressure of the atmosphere. This gradient could not have been very steep despite the fact that there was 0.40 pH difference between the two ends of the tank, since the carbon dioxide partial pressure of the atmosphere is only 0.035 ± % of an atmosphere or 0.23 ± mm. Hg.

The lateral line nerves were clipped on each side just back of the gills on the same fish used in experiments, graphs 1, 2, and 3, figure 1, and allowed to recover. "With certain exceptions, the cutaneous sensory branches of both facial and glossopharyngeal nerves are lacking in teleosts" (Kappers, Huber, and Crosby, '36). No. 4, figure 1, is a graph of this operated (with nerves to lateral line clipped) fish when tested in a carbon dioxide tension gradient comparable to experiment, graph 1. Graph 5 is of a brook trout in the identical gradient as that of the operated fish, graph 4. This fish (a rainbow trout) did not survive the clipping of the IXth and Xth cranial nerves on both sides just central to the gills. None of the fishes (rainbow trout, graph 4, figure 1, and graph 4, figure 3, and a brook trout, graph 4, figure 2, and five rainbow trout and three brook trout, not figured) with nerves on the two sides leading to the lateral lines severed were able to respond to a carbon dioxide tension gradient despite the fact that these fishes seemed otherwise to be perfectly normal. Normal fishes (rainbow trout, graphs 1 and 3, figure 1, and 1 and 3, figure 3, brook trout, graph 1 and 3, figure 2, and the other eight rainbow trout and four brook trout not figured) responded to carbon dioxide tension gradients both above and below the carbon dioxide partial pressure of the atmosphere. All controls (rainbow trout, graph 2, figure 1, and graph 2, figure 3, and a brook trout, graph 2, figure 2, and four rainbow trout and two brook trout not figured) were all typical in that they showed no preference for either end of the gradient tank.

No. 5, figure 3, is a graph of a rainbow trout that had been kept in water with a carbon dioxide tension (0.10 pH below that of the water when equilibrated with atmospheric air) higher than the carbon dioxide partial pressure of the air. The first third of the graph shows the response during the first 6 minutes, the second third, the 18th to the 24th minute and the last third, the 40th to the 46th minute of the experiment which lasted for 58 minutes. At first the fish was positive to the higher carbon dioxide tension to which it gradually changed over and became negative to the carbon dioxide tension to which it was at first positive. Two other fish that had been kept in higher carbon dioxide tension water were positive to the higher carbon dioxide tension end of the tank. However this graph was the most striking of the three. These three graphs indicate that the immediate response to carbon dioxide tension of the water depends to a large extent upon the carbon dioxide tension to which the fish is adjusted.

Various combinations of clipping the IXth and Xth cranial nerves just central to the gills were carried out on 38 rainbow trout, 28 brook trout, and 4 blue gills, *Lepomis macrochirus* Rafinesque. These with additional observations will be reported elsewhere (Powers and Clark, '42). Suffice it to state that all individuals of the three species of fishes responded similarly to each type of operation and these are summarized in the following.

1. When the IXth, or Xth or both the IXth and Xth cranial nerves were sectioned just central to the gills on one side, the fish respired approximately normally and finally died more probably due to the loss of blood as the result of the operation. The responses were not unlike those of fishes mutilated in the region of the gills, without severing the nerves, causing a comparable loss of blood.

2. When the Xth nerves were clipped central to the gills on both sides the fish respired approximately normally and died most probably due to loss of blood.

3. When the IXth cranial nerves were clipped central to the gills on both sides normal respiration was markedly modified. The rate was very much reduced taking on a weak jerky charac-

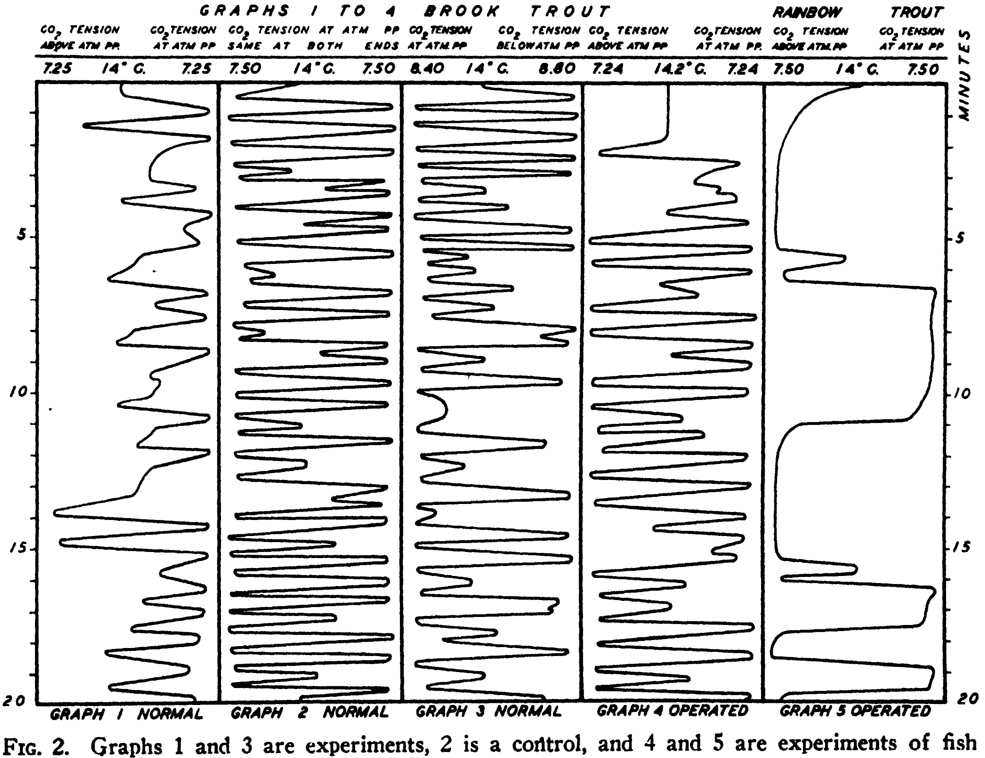

FIG. 2. Graphs 1 and 3 are experiments, 2 is a control, and 4 and 5 are experiments of fish with lateral line nerves clipped.

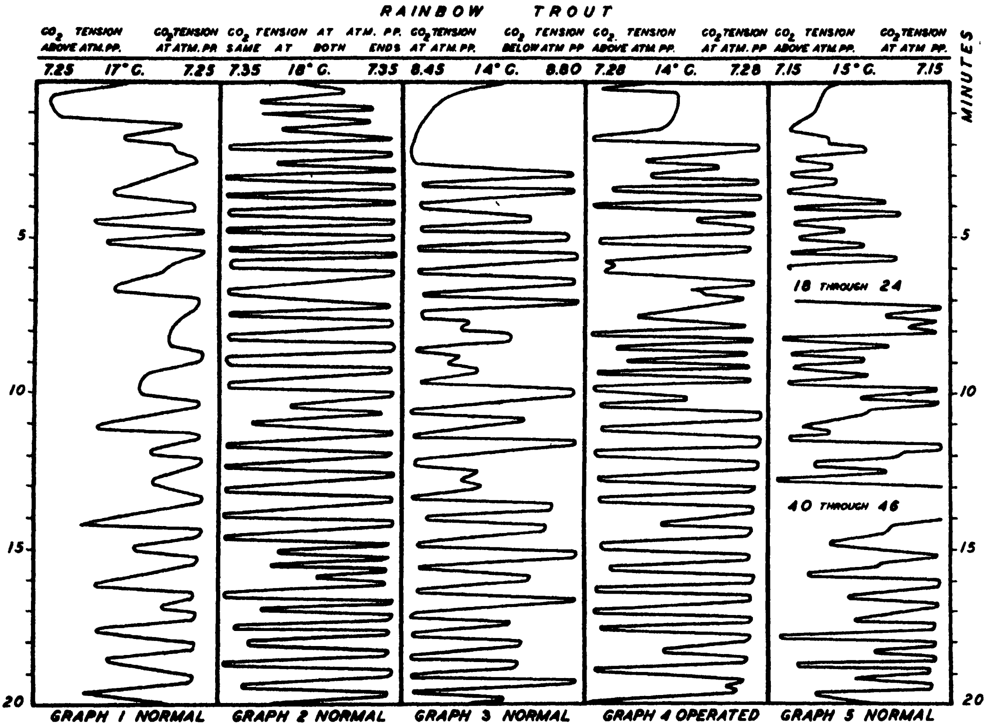

FIG. 3. Graphs 1 and 3 are experiments, 2, a control, 4, an experiment of a fish with lateral line nerves severed; and 5 is an experiment of a fish that reversed its reaction to a carbon dioxide tension just slightly higher than the carbon dioxide partial pressure of atmospheric air. The first third is for the first 6 minutes. The second third is for the 18th to the 24th minute. The last third is for the 40th to the 46th minute of an experiment that lasted for 58 minutes.

teristic and at intervals there was always an extreme gasping type of respiration. As a general rule these operated fishes died more quickly than those after other types of operations despite the fact that the loss of blood as a rule was not so great.

4. The conclusions drawn from these observations are that:

a. The IXth cranial nerves are more effective in controlling respiratory movements than the cephalic portion of the nervous system. However, the loss of blood as a result of the operation might have its effect. This is not likely the case since there is a cessation of all respiratory movements for several seconds immediately following the central clipping of both the IXth and Xth on both sides or only the IXth on both sides.

b. These operations show more clearly the inhibition effect of the IXth cranial nerves or even one alone on the gasping type of respiration that must be centered in the cephalic portion of the nervous system.

c. There is no evidence that the IXth and Xth or the IXth or Xth cranial nerve receptors (located in the gills) are effective in the response of the fish to a carbon dioxide gradient (since these fishes, the rainbow trout and brook trout did not respond when the nerves leading to the lateral lines only were severed).

SUMMARY

1. The two species of fishes tested can respond to very slight carbon dioxide tension gradients.

2. Afferent receptors excitable by carbon dioxide tension of the water are located in the lateral line organs.

3. It is suggested that a response to a carbon dioxide tension gradient is a dominant factor in the spawning migratory movements of fishes especially the salmon.

4. The IXth cranial nerves have more control over normal respiratory movements than does the cephalic portion of the nervous system.

5. The IXth cranial nerves act as an inhibitor over the gasping type of respiration which is centered in the cephalic portion of the nervous system.

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TEMPERATURE AND THE WORLD DISTRIBUTION OF CRABS OF THE GENUS *CANCER*

True decapods made their first known appearance in the Mesozoic era (205 to 60 million years ago); and the first Brachyura, or true crabs, appeared about the middle of the same period. True decapods had been in existence for approximately 140 million years when the genus *Cancer* made its first known appearance in the Eocene epoch, 60 million years ago (Calman, '11).

The genus *Cancer* is entirely marine. It has a world-wide distribution and is represented by the 19 living species listed in table I. This list is thought to be complete since it is the result of an extensive search through faunal lists, the records of exploring expeditions, and the unpublished personal records of Dr. Mary J. Rathbun of the Smithsonian Institution. The distributional data are chiefly from Rathbun ('30a).

Limits of Distribution of Cancer

The world-wide distribution of *Cancer*, as presented above, is indicated in figure 1. It will be observed that the genus inhabits the temperate zone and that it is practically absent from the tropics. As marine organisms, crabs are necessarily dependent upon water temperatures and these in turn are roughly correlated with air temperatures. The chief differences between mean air and surface water temperatures are a consequence of warm and cold ocean currents. In warm regions surface water is usually warmer than water at greater depths; the converse is true in colder regions.

The 75° F. surface water isotherm corresponds closely to the *southern limit* of distribution in the northern hemisphere and to the *northern limit* in the southern hemisphere. The presence of *Cancer* along the northwestern coast of South America may be attributable to the lowering of temperature caused by the cold Humboldt current which sweeps up from the south and which is also thought to help explain the presence of penguins in the Galapagos Islands. The occurrence of *C. borealis* just south of Dry Tortugas, Florida, is probably explained by the fact that the few specimens obtained were secured at depths of 112 to 158 fathoms where temperatures would be considerably below the corresponding surface regions.

The northern distribution in the northern hemisphere and the southern distribution in the southern hemisphere are probably limited by cold and by drift ice. In the northern hemisphere the genus *Cancer* is not known to occur north of latitudes having an annual mean surface water temperature of 40° F. The Canadian Arctic Expedition of 1913–1918 failed to find any species of *Cancer* in Arctic North America although extensive collections of Crustacea were made and were later identified by Rathbun (Rathbun, '19). Since *Cancer* in colder regions is characteristically found in shallow water it would necessarily suffer from cold and from shore ice. Its absence from these regions is, therefore, not surprising.

Temperature and the Past Distribution of Cancer

If the writer is correct in believing that the present world distribution of *Cancer* is principally limited by temperature, then it is possible, if not probable, that this has been the case for a long period of time. In this event the finding of fossil crabs of this genus in various parts of the world might furnish a rough indication of water temperatures at various times in the past for the regions in which the fossils were found. A list of the fossil *Cancers* of North America (Rathbun, '26 and '35) with the geological period of each is given in table II. In

TABLE I. *Table showing the distribution of the species of the genus Cancer*

Species	Distribution
Western North America	
C. productus	Kodiak Is., Alaska, to Laguna Beach, California.
C. oregonensis	Pribilof Islands and Rat Islands, Alaska, to Santa Barbara, California. A shallow water form.
C. pygmaeus [1]	La Jolla, California, to Gulf of California, Mexico. Also Japan, Korea, and China (amphioetus of authors).
C. antennarius	Tomales Bay, California, to the west coast of Lower California, Mexico; as far south as San Geronimo Island, Magdalena Bay.
C. branneri	Granite Cove, Port Althrop, Alaska, to Santa Catalina Island, California.
C. jordani	Humboldt Bay, California, to San Geronimo Island, Lower California, Mexico.
C. anthonyi	Monterey Bay, California, to Magdalena Bay, Lower California, Mexico.
C. gracilis	Prince of Wales Island, Alaska, to Playa Maria Bay, Lower California, Mexico. Shore to 56 fathoms.
C. magister	Unalaska, Alaska, to Monterey Bay, California. Shore to 50 fathoms.
Eastern North America	
C. irroratus	Labrador to South Carolina. In shallow water in the north; in deeper water in the south.
C. borealis	Bermudas and Nova Scotia to Florida; just south of Dry Tortugas, Florida (112 to 158 fathoms). Shore to 435 fathoms.
Western South America	
C. edwardsii	Ecuador, Peru, Chili; as far south as Trinidad Channel.
C. plebejus	Callao, Peru, to Port Otway, Magellan Territory, Chili. To a depth of 6 fathoms.
C. porteri	Bay of Panama to Valparaiso, Chili. 210–286 fathoms.
C. polydon	Bay of Ancon, Ecuador, to the Island of Chiloe, Chili.
Europe	
C. pagurus	Northwestern Europe from Norway and Germany to Portugal (*C. luederwaldti*).
Asia	
C. japonicus	Tokio Bay, Japan.
C. gibbosulus	Hokkaido and northeastern coast of Nippon, Japan.
C. pygmaeus	Hokkaido, Japan, to Korea and the Gulf of Pechili, China; California to Mexico.
Australasia	
C. novae-zealandiae	New Zealand and Tasmania; Mentone, Port Phillip, Australia.

[1] Miss Rathbun informs me that *C. pygmaeus* Ortmann takes precedence over *C. amphioetus.*

TABLE II. *North American fossil crabs of the genus Cancer*

Species	Locality	Geological period
Eastern North America		
C. proavitus	Martha's Vineyard, Massachusetts	Miocene
C. irroratus	Calvert County, Maryland	Miocene
" "	Cape May County, New Jersey	Pleistocene
" "	St. Marys County, Maryland	Pleistocene
C. borealis	Old Grove wharf, James River, Virginia	Miocene
Western North America		
C. fissus	South of Coalinga, Fresno, California	Pliocene
C. urbanus	Los Angeles County, California	Pliocene
C. anthonyi	Spanish Bight, San Diego Bay, California	Pleistocene
C. branneri	San Pedro and Long Beach, California	Pleistocene
C. gracilis	Santa Monica to San Diego Bay, California	Pleistocene
C. jordani	Santa Monica to San Pedro, California	Pleistocene
C. magister	Northeast of San Pedro, California	Pleistocene
C. productus	Santa Monica, California, to San Quentin Bay, Lower California, Mexico	Pleistocene
C. bainbridgensis	Sandstone beach at Bean Point, Bainbridge Island, Puget Sound, Washington	Upper Oligocene
C. gabbi	Martinez or Clayton, Contra Costa County, California	Eocene

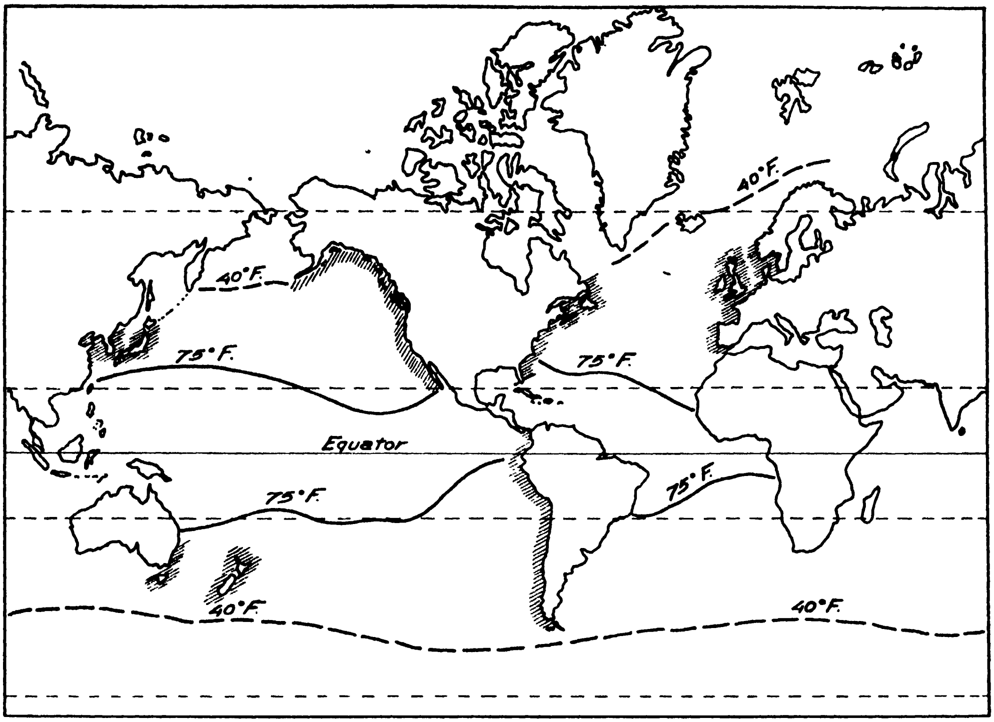

FIG. 1. World map showing the relationship between the mean surface water isotherms and the distribution of the genus *Cancer*.

addition to these, Glaessner ('29) lists 11 species found in various parts of the world with two others not specifically named, but which almost certainly belong to the genus. He further includes 17 other species more or less doubtfully referred to *Cancer.*

SUMMARY

Crabs of the genus *Cancer* are known to have been in existence since the Eocene epoch and the 19 living species have a world distribution roughly bounded by the surface water isotherms for 75° F. and 40° F. If fossil members of the genus were similarly limited by temperature they would furnish an indication of water temperatures for past geological periods.

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SEASONAL CHANGES IN THE OSTRACOD FAUNA OF TEMPORARY PONDS[1]

During the spring and early summer of 1940, the writer made semimonthly collections of ostracods from several temporary ponds in Champaign County, Illinois. These collections were used as the basis for a study of the seasonal changes in the ostracod fauna from the time ostracods appeared in early March until the ponds became dry about the middle of July.

The ponds selected for study include: (1) the prairie ponds near Seymour, Illinois; (2) pond 1, Busey's pasture, Urbana, Illinois; (3) pond 2, Busey's pasture, Urbana, Illinois; and (4) pond 7, Urbana, Illinois. The numbers assigned serve to identify certain ponds used for study by ecology classes at the University of Illinois. The ponds from which collections were made are all temporary in nature, normally becoming filled with surface water during the prevernal season or earlier and drying up about the beginning of the serotinal season (near the middle of July). In the case of the Seymour ponds, the data from several very small ponds have been pooled since there were no apparent differences in collections made on the same day from the various ponds. The other ponds differ considerably and are discussed individually.

In the ponds at Seymour, *Candona simpsoni* (immature when first observed) was the first species to be seasonally present, appearing at least by the middle of March with *Candona fossulensis* and *C. distincta* entering about the first of April. Later in the same month *Candona indigena, C. biangulata,* and *Cypricercus reticulatus* were found. Most of the Candona species have a short life span and disappear from the collections near the first of May except *C. simpsoni* which, along with *Cypricercus reticulatus,* persists until after the middle of May. Near the middle of May, *Cypridopsis vidua* becomes abundant and from shortly after the first of June until about the middle of July, when the ponds become completely dry, it is the only species present.

Pond 1 differs considerably from the Seymour ponds by being larger and well shaded by trees in contrast to the Seymour ponds which are prairie ponds, smaller, and relatively unprotected. Here again, however, *Cypricercus reticulatus* (immature when first observed) is confined to the vernal season and drops out by the last of May. *Candona indigena* is present on the same date as in the ponds at Seymour and *Cypridopsis vidua* is found during May, June, and July. In addition to the species which are the same as in the ponds at Seymour, *Cypria turneri* was present, as if by accident, in a single collection in March. *Candona simpsoni,* which was collected at Seymour in March, April, and May, was found in pond 1 only in a single collection on June 9.

The data on seasonal changes in pond 2 are incomplete since collections were not started until May first. This pond is the deepest and most extensive of those studied and, had the collections been started earlier, might have been the most profitable. The data could not be completed in the spring of 1941 since there was little rain and the pond filled up too late to be of value in this study. One of the main peculiarities of the species in this pond is that *Cypria turneri* was present from at least the first of May until the pond dried up in July. *Candona simpsoni* and *Cypricercus reticulatus* also continued until June, remaining longer than in the Seymour ponds as a result possibly of a lower temperature brought about by the shaded condition of the pond and the greater mass of water. *Cypridopsis vidua* disappeared before the collection of July 10, when the pond was reduced to a mere "mud-puddle." *Candona suburbana* was found in late May and early June and two species of Cypria, *C. obesa* and *C. ophthalmica,* were present only in the collection of June 9.

Pond 7, which is formed in a depression in a pasture, is more like the Seymour ponds than the other ponds but there was some difference in species of ostracods present. Only four species were found in this pond, two of which were also common to all of the other ponds. *Cypricercus reticulatus* (immature when first collected) was present here when the first sample was taken in early March and dropped out before the May 4 collection. The life cycle, a single generation, was completed here earlier than in the other ponds. During June and July, only *Cypridopsis vidua* was present. In May only *Cypria maculata,* which was not found in any of the other ponds, and *C. ophthalmica,* which was also seen in pond 2, were present.

From the present study, it is possible to draw a few general conclusions with reference to the ecology of ostracods inhabiting temporary ponds. In the first place, the life cycle of many species is short, much shorter, in fact, than the life of the pond in normal years would necessitate. This is particularly true of several species of Candona, *C. indigena, C. biangulata, C. fossulensis,* and *C. suburbana.* Each of these species occurred in not more than two successive collections which would limit the life span to perhaps not greater than one and one-half months. In three of the four species mentioned, the life span could be but little over one month since the species appeared only in a single col-

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[1] Contribution from the Zoological Laboratory of the University of Illinois.

TABLE I. *Seasonal changes in the ostracod fauna of temporary ponds*

(Table showing the dates on which different species of ostracods were collected from each of the four ponds. The presence of a species in the collection is indicated by "x" while "n" indicates that no collection was made on the date given. Collections marked "*" were made on March 20 instead of March 17. All dates refer to 1940.)

	Mar. 9	Mar. 17	Apr. 1	Apr. 15	May 4	May 18	June 9	June 22	July 10
Seymour Ponds									
Candona simpsoni Sharpe 1897	n	x	x		x	x			
C. fossulensis Hoff 1942			x						
C. distincta Furtos 1933			x		x				
C. indigena Hoff 1942				x					
C. biangulata Hoff 1942				x					
Cypricercus reticulatus (Zaddach 1844)				x	x	x			
Cypridopsis vidua (O. F. Müller 1776)						x	x	x	x
Pond No. 1									
Cypria turneri Hoff 1942	n	x*							
Cypricercus reticulatus (Zaddach 1844)		x*	x	x	x	x			
Candona indigena Hoff 1942				x					
Cypridopsis vidua (O. F. Müller 1776)					x	x	x	x	x
Candona simpsoni Sharpe 1897							x		
Pond No. 2									
Cypricercus reticulatus (Zaddach 1844)	n	n	n	n	x	x	x		
Candona simpsoni Sharpe 1897					x	x	x	x	
Cypria turneri Hoff 1942					x	x	x	x	x
Candona suburbana Hoff 1942						x	x		
Cypridopsis vidua (O. F. Müller 1776)						x	x	x	
Cypria obesa Sharpe 1897							x		
Cypria ophthalmica (Jurine 1820)							x		
Pond No. 7									
Cypricercus reticulatus (Zaddach 1844)	x	x	x	x					
Cypria maculata Hoff 1942					x	x			
Cypria ophthalmica (Jurine 1820)					x	x			
Cypridopsis vidua (O. F. Müller 1776)							x	x	x

lection. This means that, in this habitat at least, there is no more than a single generation each year. In the case of *Cypricercus reticulatus,* the life span may be as great as two months, but the writer knows from observations that there is a single generation per year. This species is very slow to mature; it appears in early spring and disappears after about two months. The eggs apparently remain unhatched during the summer, fall, and winter with the young appearing in early spring, usually March (Hoff, '42).

Some of the species listed here from these temporary ponds are typically temporary water species. This is particularly true of *Cypricercus reticulatus* and most of the Candona species. *Cypria turneri* and *Cypria ophthalmica* are very common in temporary waters but are by no means confined to this kind of habitat.

It is frankly impossible to tell from the data why certain species appear in some ponds and different species in other ponds. There may be some limiting factor operating, but, from the similarity in general appearance of the ponds, each should offer a suitable habitat to the same species of ostracods, especially since ostracods tolerate a wide variation in most of the factors which could operate in limiting distribution. The occurrence of some forms in one pond and other forms in another pond may be due entirely to random dissemination. The species best adapted to life in temporary ponds probably have eggs which are easily carried by the wind or disseminated effectively by other means. As a result, these forms are found in the majority of temporary ponds. In contrast to this distribution which may be at random, it is entirely possible that environmental factors may have some influence upon the seasonal appearance, development, maturity, and death in some of the species. Temperature may play a part in regulating the appearance of species through control of the time necessary for hatching from the egg. There must be some influential factor in operation or the very common and cosmopolitan species, *Cypridopsis vidua,* would not appear in every pond after the first of May and be, in almost every instance, the last ostracod to disappear before the pond becomes dry. Wolf ('19) found that temperature is a limiting factor in the seasonal appearance of certain ostracod species in Switzerland. However, if temperature were always important as a controlling factor, *Cypricercus reticulatus* would not appear as early as March 9 in pond 1 and not until April 15 in the Seymour ponds especially since the Seymour ponds are not sheltered from the sun and should become warmer than the forest ponds. It is possible then that a factor other than temperature controls the seasonal appearance of some species.

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THE EFFECT OF CATTLE GRAZING ON KOA REPRODUCTION IN HAWAII NATIONAL PARK

Cattle grazing has had severe effects upon many types of Hawaiian vegetation. Grassland now occupies extensive lands where luxurious forests formerly stood. The prominent and important native tree, koa (*Acacia koa*), has proved particularly susceptible to cattle damage, and in many localities remnant koa forests are regressing rapidly toward extinction. The manner in which grazing acts unfavorably upon koa has been the subject of casual remarks in the literature of Hawaiian forestry, but the subject heretofore has received no systematic analysis.

Such a study will be presented in the following pages. We shall analyze the most conspicuous process by which cattle have damaged pure koa forests in past decades on the middle slopes (4000 to 6000 feet) of Mauna Loa in Hawaii National Park. This process is the suppression of koa reproduction by grazing.

Cattle Damage Long Recognized

An anonymous writer (1856) described the killing of the forest of the Waimea plains in the half century subsequent to the introduction of cattle in 1793. The writer stated: "It is in the memory of many foreigners now living there when the whole of these plains were covered with a thick wood, to the very edge of the slope. Where hardly a tree is to be seen for miles, we were informed by an old resident, that twenty-five years ago he lost himself with his team in the woods." He described the manner of forest destruction: ". . . whilst the old trees die of age, no young ones are seen taking their places, as during the last 30 or 40 years, the cattle have eaten or trodden them down." In the same year William Hillebrand (1856) delivered a resounding address on the necessity for forest conservation, pointing out that serious encroachments upon the domain of the forest had been made and that "of all destroying influences man brings to bear on nature, cattle is the worst."

The specific effect of cattle on koa has also been mentioned. R. S. Hosmer ('06) recommended fencing cattle from logged koa tracts to insure establishment of koa reproduction after lumbering. This was a recognition of the suppressive effect of cattle grazing on koa reproduction. C. J. Kraebel ('22) recorded that in the Honouliuli forest reserve on Oahu, where cattle had been excluded for a number of years, koa groves were developing with surprising speed. He claimed that elsewhere great improvement would result within a few years if cattle should be removed.

C. S. Judd ('18) discussed extensive reductions of forested area on various Hawaiian islands, imputing much responsibility to cattle. Judd ('24, '27) described the native Hawaiian forest as a delicately balanced association of trees and ground cover plants. The former are shallow-rooted, the latter make up a dense, moisture-holding structure of shrubs, vines, ferns, and many small plants. He believed cattle had done far more to upset this balance than any other agency. He held that removal of the undergrowth by cattle led to tree root damage from changed soil and moisture conditions. The trees became subject to attack by destructive insects and fungi. The invasion of foreign grasses and plants prevented tree reproduction. His emphasis was upon the serious consequences resulting from destruction of the native ground cover.

We regard the direct effects of grazing on reproduction as more destructive to koa in the Hawaii National Park than the indirect effects from loss of the native ground cover. If ferns and small, delicate plants were formerly abundant in the understory of the koa groves, they have now all but disappeared. Estimates of ground cover on 18, one-tenth-acre quadrats were made in August 1941. The principal understory plants were found to be 25 per cent Hilo grass (*Paspalum dilatatum*), 20 per cent velvet grass (*Holcus lanatus*), 10 per cent Bermuda grass (*Cynodon Dactylon*), 9 per cent thimbleberry (*Rubus rosaefolius*), 7 per cent orchard grass (*Dactylis glomerata*), and 7 per cent hairgrass (*Deschampsia nubigena*). All except the last named are exotic. Since many of the mature koa trees appear to be healthy, the replacing of the original ground cover under the trees by exotic plants has not in itself been fatal. This is also indicated by vigorous young growth in groves protected from cattle grazing. Therefore, the present analysis is limited to the direct effects of grazing upon reproduction, as opposed to the indirect effects from loss of the native ground cover.

CHARACTER OF THE VEGETATION

The plant formation, soil, and climate of this region have been described by Robyns and Lamb ('39). The vegetation is xerophytic parkland formation. Open grassland borders and separates closed koa groves. Other trees occur throughout the area but in small numbers compared to the koa. Native shrubs occur widely on open land.

The koa appears to reproduce almost entirely by means of root suckers. Of the many young koa plants examined in the study, not one was found to be a seedling. MacBride[1] ('37) determined that up to 80 per cent of the koa seeds may be destroyed in the pods by the koa seed moth (*Cryptophlebia illipeda* var. *fulva*). Many vigorous suckers arise from the buried and exposed roots of a single tree. The root system of the mature koa is shallow and extensive, spreading out radially from the base of the tree up to 100 feet or more. In three cases, suckers were seen 50, 90, and 95 feet away from the base of isolated koa trees. Suckers develop into healthy trees three to six inches in diameter at breast height in five or six years. As yet, no analysis of the natural means by which Hawaiian koa reproduces and establishes itself has appeared in the literature.

HISTORY OF GRAZING

It is believed that the Mauna Loa slopes in question have been continually grazed by wild and domestic stock for more than a century prior to 1927, when the region was incorporated into the Hawaii National Park. At this time, the practice of goat and pig control was started. These animals were largely eliminated from the area where the study was made. Moderate cattle grazing continued until October 1940, with a small number of horses and mules continuing on the land up to the present. The effect of stock other than cattle upon koa reproduction is considered to have been negligible in recent years.

METHODS

Plots and Quadrats.—Six plots ranging from two to seventeen acres in area were selected in typical koa groves. The six plots fell into three pairs according to their grazing history. The first pair had been fenced from cattle for six years, the second pair for only six months, and the third pair was grazed through the entire time of the study. Each pair of plots consisted of one located in a senile and decadent grove, and one in a healthy and vigorous grove. All six plots were within a radius of one-half mile of each other.

Each plot was studied by quantitative analysis of the reproduction in three, one-tenth-acre quadrats located to represent typical conditions at the edges and center of the plot.

Koa Size Classes.—Counts were made of koa individuals on each quadrat. Three size classes were used, as set forth in table I. The size limits were chosen to separate the mature trees and the two size groups of reproduction which field work showed to be distinct and conspicuous. Thus, the young suckers which had sprouted and grown in the six-months-protected areas fell into class one, while the saplings on the six-years-protected areas (mostly six years of age) fell into class two. The old trees fell into class three. These were all much larger than the largest saplings in the plots, indicating a great difference in age. Hereafter, the reproduction falling in class one will be spoken of as "suckers," that in class two as "saplings," and that in class three as mature or senile trees.

TABLE I. *Size classes of koa*

Koa size class	Size limits		Approximate age of reproduction
	Lower	Upper	
1	no lower limit	30 in. high	0 to 6 mo. (suckers)
2	30 in. high	6 in. d.b.h.*	6 mo. to 6 yrs. (saplings)
3	6 in. d.b.h.*	no upper limit	typically mature or senile trees

* Diameter at breast height.

RESULTS

The data are presented in table II. A comparison of counts on healthy and decadent plots was made. Those with like grazing history

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[1] **MacBride, O. C.** Unpublished manuscript. Insect pest survey of Hawaii National Park.

TABLE II. *Number of koa plants by size classes recorded on plots of different grazing history. Three tenth-acre quadrats were used on each plot*

Protection period for plots	Healthy grove			Decadent grove			Total		
	Size class			Size class			Size class		
	1	2	3	1	2	3	1	2	3
6 years	5	373	5	9	184	14	14	557	19
6 months	136	0	11	287	0	8	423	0	19
None	4	0	7	37	0	11	41	0	18

showed similar distribution of the three size classes. In plots protected from cattle for six years, a large number of saplings was present. The saplings were fairly uniform in size, estimated to average 12 feet in height and three inches in diameter at breast height. Nearly all of this reproduction appeared immediately or shortly after the cattle were excluded from the plots in 1935, and the survival rate was high (figure 1). Plots one and two belong in this category, and the six quadrats of the two plots together showed a total of 557 saplings. In the plots protected for only six months, saplings were conspicuously absent. No reproduction other than young suckers was present, but of this there was an abundance. Plots five and eight belong in this category, and on their six quadrats 423 suckers were found. The suckers were of recent development, as shown by the tender and pubescent character of their leaves. They showed no signs of being stunted (figure 2). In the plots upon which cattle grazed the entire time, there were no saplings and only a small number of young suckers. Plots seven and nine represent this condition, and upon their six quadrats were found only 41 suckers. Browsed and trampled by cattle, they were in no case over six inches in height (figure 3).

FIG. 1. Koa reproduction in a decadent grove protected from cattle grazing for six years. This reproduction, now sapling size, appeared immediately or shortly after the grove was fenced in 1935. April 25, 1941, H. N. P. photo.

FIG. 2. Koa sucker reproduction from decadent koa trees after one year of protection from grazing. A decadent grove, protected nearly seven years, with its understory of saplings may be seen in the background beyond the fence. January 24, 1942, H. N. P. photo.

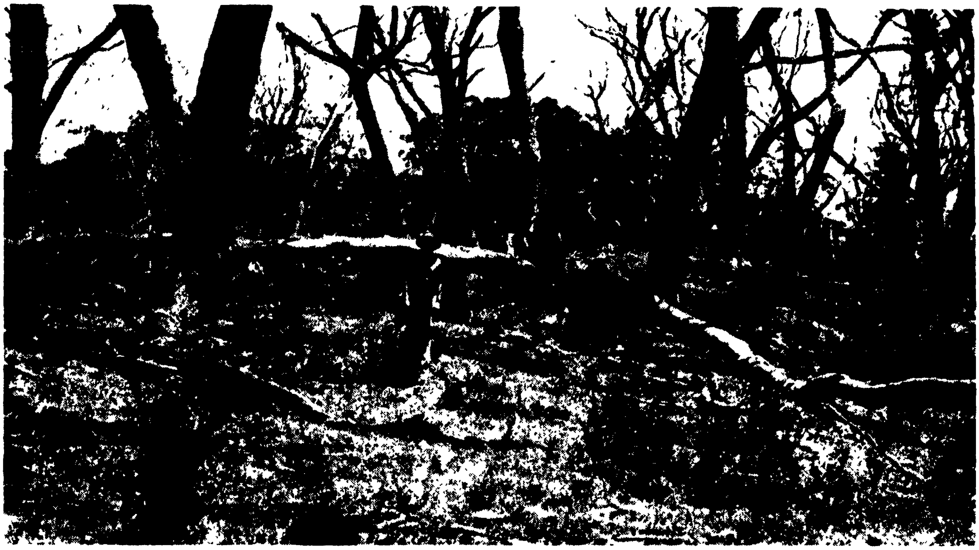

FIG. 3. A continuously grazed, decadent koa grove showing the absence of established reproduction. The 37 nibbled and stunted suckers recorded on three tenth-acre list quadrats in this grove were less than six inches high. April 18, 1941, H. N. P. photo.

DISCUSSION

The uneven representation of size classes on the various plots is to be accounted for entirely on the basis of their grazing history. Where the influence of cattle had been removed from the land for six years, healthy stands of saplings had become established where previously there had been none. Where this influence had been removed for six months, an abundant growth of suckers was present. On land continually grazed virtually all reproduction was suppressed. Cattle did not inhibit the koa trees from sending out suckers but continually prevented their successful establishment.

A considerable portion of this region is now open grassland but still has many dead koa trees upon it. The disposition of these relics implies that they once formed large groves of koa similar to those still standing nearby. The cause of death of the old trees may have been fire or some subtle, unrecorded process. However, it is reasonable to attribute to cattle the failure of both seedlings and suckers to perpetuate these groves.

This study has strengthened the conclusion that cattle are a destructive agency in the Hawaiian koa parkland. It has shown that where it is desired to perpetuate an area of original koa forest, it will be necessary to protect koa reproduction from cattle. Though the study was limited to the suppression of reproduction, this is not considered the only unfavorable effect of cattle upon the koa groves.

SUMMARY

1. The relation of cattle grazing to the establishment of koa reproduction in Hawaii National Park was studied by quantitative analysis of sample plots (1) grazed previously to but not during the past six years, (2) grazed previously to but not during the past six months, and (3) grazed the entire time.

2. A large number of saplings was present in the six-years-protected plots, where there was no reproduction previous to the fencing. A large number of root suckers up to 30 inches in height appeared in the plots protected for six months. Only nibbled suckers less than six inches in height were present on land grazed through the entire time. These differences can be explained wholly on the basis of the effect of cattle browsing on the reproduction. Where cattle grazed no reproduction was established; where cattle were excluded reproduction was successful and vigorous.

3. The suppression of reproduction by cattle accounts for the absence of established koa reproduction throughout the koa parkland and for the failure of koa reproduction to perpetuate the extensive koa groves which once existed over a large portion of the region.

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A METHOD FOR MEASURING UTILIZATION OF BLUESTEM WHEATGRASS ON EXPERIMENTAL RANGE PASTURES

Before the effects of varying grazing use on range plants can be fully recognized and the proper degree of use specifically defined, a reliable and objective method for measuring degrees of utilization is essential. Various methods have been tried and rejected as unsatisfactory for experimental range pastures at the U. S. Range Livestock Experiment Station near Miles City, Montana.[1] Since 1938, a method for making utilization surveys has been under development which gives promise of meeting the essentials for short-grass ranges better than anything yet tried at this station. By this method, systematic measurements and observations are made for a few important key species located along a network of transects through pastures grazed at different intensities.

The six summer cattle pastures vary from about 90 to 195 acres and all radiate from a central well. Two pastures are grazed lightly, two moderately, and two heavily. The transects used for locating sampling "stops" extend along chords of concentric circles drawn with the well as center. The radii of the circles increase progressively by 10 chains so that the chords are at approximately this same interval. This spacing of transects provides samples for each pasture at equal distances from the central well. Observations are recorded at three circular sampling units or "stops" for each chain of transect. The central point of each sampling stop is established by markers attached to the chaining tape at 15, 50, and 85 links, respectively. This spacing of transects and sampling units provides an average of about three observations per acre for each species to be measured. This has been intensive enough to reveal differences in degree of grazing that were so slight as to be unnoticeable by observation. Differences of less than 5 per cent in the final utilization percentages were revealed when stubble height averages for odd- and even-numbered sampling stops were compared. This indicates that fewer than three observations for a given species per acre may provide satisfactory results for most administrative uses. Where it is desired to have very detailed information for individual subtypes or other areas of small size, more frequent observations may be necessary.

FIELD PROCEDURE AND DATA COLLECTED

Three of the most important and widely distributed forage species on the experimental ranges are considered as key species in these surveys. For each of these, the remaining height of grazed plants (stubble), a tally of grazed and ungrazed plants, and certain other information are recorded during the survey. Appropriate specifications were drawn up to define a plant for each species. Less detailed data are also recorded for associated but less important species. For the sake of brevity, the following detailed description of the procedure will be confined to one species—bluestem wheatgrass (*Agropyron smithii*)—which is rather uniformly distributed. Each bluestem plant usually consists of a single stem though two or three stems occasionally occur. It also appears to be the most sensitive single indicator of grazing intensity by cattle on these experimental pastures.

In following the web of transect lines through the various pastures, two men make a crew. The head chainman serves as compassman and recorder while the rear chainman calls out measurements and observations. Each sampling unit is limited to a circle with a radius of one meter centering at the link on the chain previously marked for this purpose. At each such stop, the observer locates the bluestem plant nearest the center of the sampling unit and determines whether it is grazed or ungrazed. If one is present and grazed, he measures the residue, or stubble, and its height is recorded on the data sheet. If the nearest plant is wholly ungrazed, it is so recorded. If the nearest bluestem plant is a stubble, partially or wholly protected from further grazing by cactus, sagebrush, or other obstacle, this fact is recorded. The stubble height measurement is then made on only the portion that extends above the obstacle, rather than to the ground level as is done for those plants that are not protected.

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[1] Range research work at the U. S. Range Livestock Experiment Station is conducted by the Forest Service in cooperation with the Montana Agricultural Experiment Station and the U. S. Bureau of Animal Industry.

[2] The authors wish to express gratitude to Harold St. John of the University of Hawaii and Edward Y. Hosaka of the B. P. Bishop Museum for reading the manuscript.

DATA COMPILATION

From the field sheets, average stubble height of grazed bluestem plants is computed separately for each transect, subtype, and pasture. From the record showing number of ungrazed and grazed plants observed, the percentage of grazed plants is calculated. By means of a height-weight curve, average stubble height is converted to per cent of weight remaining on grazed plants to the ground level. The difference between this figure and 100 per cent represents the portion of the plant that has been removed by grazing. This percentage use of grazed plants, multiplied by the percentage of all stems that have been grazed, gives the total per cent to which bluestem has been removed.

CONSTRUCTION OF HEIGHT-WEIGHT USE CURVE FOR BLUESTEM WHEATGRASS

The height-weight relationship has been investigated by Lommasson ('38), Crafts ('38), and others. It is well established that culmed plants have different height-weight relationships from culmless plants. Furthermore, the ratio of culmed to culmless stems varies widely from year to year. Also, it is frequently impossible to determine from a grazed stubble whether the plant was of the culmed or culmless form before it was grazed. This calls for a curve that will show the proper relationship and proportion for culmed and culmless forms for the site and year in question. Such a combination curve has been made up in the following manner:

In July or August when growth of bluestem was complete, 100 culmless ungrazed plants were collected at random for the various subtypes and pastures to be surveyed later. These sample plants were clipped at the ground level and afterwards in the laboratory were cut into 2½-centimeter segments, beginning at the base. These various segments from the 100 plants were then air-dried and weighed. A similar procedure was then followed for 100 mature culmed plants. At this same time the ratio of culmed to culmless plants on the pastures was determined by a simple sampling procedure. Because some of the original plants had by that time been grazed by cattle that had been on the summer pastures for about 2½ months or nearly half the grazing season, the remaining ungrazed plants may have averaged slightly taller or shorter provided cattle selected plants that were shorter or taller than the average. It was believed, however, that this possible source of a slight error was less objectionable than samples from another area, or from protected plots where site differences might cause even a greater difference in average height.

From weight data for corresponding segments of culmed and culmless plants in the proper ratio for the season, a combination height-weight relationship was obtained and a curve constructed. Stubble heights are shown in centimeters on one axis and the corresponding percentages of total weight removed on the other axis. For convenience in computing actual grazing use from the curve, a utilization table is made from the curve showing percentage of use that corresponds to various stubble heights. A part of this derived table follows:

Stubble height in centimeters	Per cent bluestem use
1	94.0
2	88.0
3	81.0
4	73.5
5	65.0
6	56.5
8	41.0
etc.	

ADJUSTMENT OF CURVES FOR USE IN SUCCEEDING YEARS

The heights attained by ungrazed bluestem plants vary somewhat from year to year because of different growth conditions. This necessitates either construction of new height-weight curves or adjustment of existing curves. The latter method has been followed until a new curve from growth in succeeding years can be constructed for comparisons. Such a comparison will be necessary to determine whether a material difference in utilization is shown when an adjusted curve is used as compared to using one constructed directly from the current year's growth.

Both the culmed and culmless curves originally constructed are adjusted on a percentile basis. For example, assume that ungrazed culmless bluestem plants grew, when fully extended, to an average height of 24 centimeters in 1939 and from the height-weight curve constructed in that year an average stubble height of 12 centimeters (50 per cent of average height) represented 64 per cent of total original weight. Then, if un-

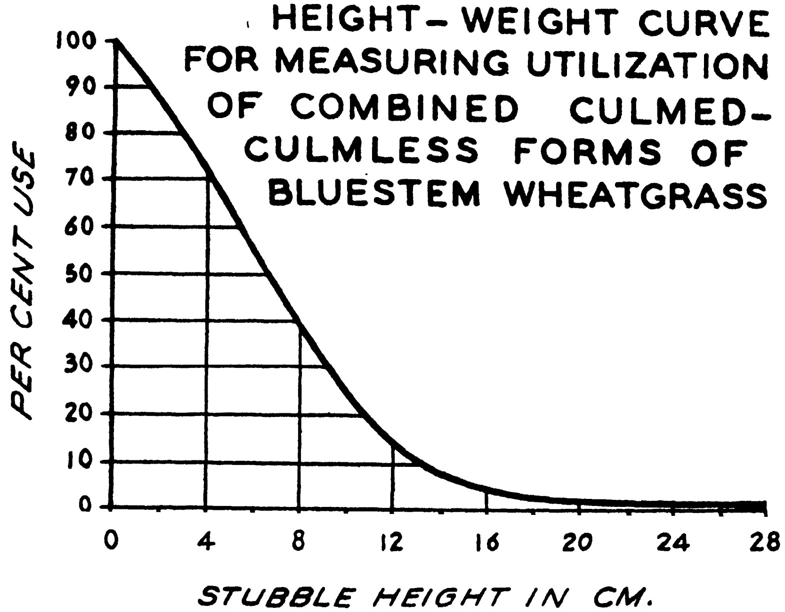

Fig. 1.

grazed culmless bluestem grew to an average height of only 20 centimeters in 1940, an average stubble height of 10 centimeters (50 per cent of average height) is assigned that same percentage of total weight (64 per cent), and likewise for each 10 per cent interval of ungrazed height. The original culmed curve is adjusted in the same manner. The separate adjusted culmless and culmed percentile weights for various stubble heights are then combined in the proper ratio to produce the adjusted culmed-culmless height-weight curve applicable to the current year. Figure 1 is the curve used in 1940 for bluestem wheatgrass after such an adjustment was made on the curve constructed and used in a previous year. It is probable that this method of adjustment would involve a substantial error if used on certain grasses that have a growth form quite different from bluestem.

A procedure similar in purpose to that just described for bluestem has been followed for two other key species, blue grama (*Bouteloua gracilis*) and niggerwool (*Carex filifolia*). Growth forms for these two species are so different from bluestem wheatgrass as to require adaptations in details of recording field data and in the construction of curves which will not be described herein. The aim, however, has been to get an estimate of use based on the percentage of grazed plants and average stubble heights just as for bluestem. Percentage of plants grazed and average stubble height have been derived for certain other associated species for a check, but their limited distribution and importance, or other limitations, have not justified considering them as key species requiring construction of curves.

Discussion and Conclusions

The fact must not be overlooked that this is an indirect method of measuring forage utilization. It is based wholly on the portion of key species remaining on the ground at the close of the grazing season, rather than on the portion actually grazed. No method has been devised for direct measurements of forage consumed by livestock, although periodic animal weights are an indirect reflection of amount used. Furthermore, the exact degree of utilization for all range forage produced cannot be specifically determined when the residues for only a few of the most important forage species are measured. This method also reveals differences in utilization due to topography, distance from water, etc., which are not otherwise evident.

Differences in degree of utilization as determined by this method have also shown a close relationship with calf weight gains from pastures grazed at varying degrees. Cows from the closely grazed pastures have produced an average of approximately 50 pounds per year less weaning calf weight than those on pastures utilized less closely. A similar method has been used in measuring utilization on sheep pastures and various important differences in grazing habits of unherded sheep and cattle were revealed by it. Sheep damaged the range severely on certain areas by grazing more closely than cattle but left more unused forage at other places.

In regular administrative practice, it is seldom necessary to have refined measurements of utilization on every portion of a large range area because some parts may be clearly under-utilized and other parts obviously overgrazed. Accurate measurements are most essential on those limited areas which closely approach a critical degree of use even though this critical point may not yet be exactly defined. Even a comparatively few definite measurements on these limited areas by this method will be more reliable than generalizations based on observations alone. Increased reliability of results may be had by increasing the intensity of sampling. With suitable adaptations, the method offers considerable promise for use in grazing administration as well as for range research work. The range manager who can determine the actual use with greater reliability will be able to decide more quickly and with greater confidence as to the relative merits of various degrees of grazing and other range management practices.

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SEASONAL ROOT DEVELOPMENT OF SAGEBRUSH (*ARTEMISIA TRIDENTATA* NUTT.) IN RELATION TO RANGE RESEEDING

The improvement of depleted sagebrush ranges in the Intermountain region by artificial reseeding with adapted forage grasses provides a promising means of increasing the productivity of millions of acres of deteriorated range land. Numerous trials have shown that seeding in moderately dense sagebrush will not produce satisfactory grass stands unless some reduction in the density and vigor of the sagebrush is accomplished before or during the seeding operation. If the sagebrush is killed or weakened by railing, disking, plowing, scarifying, or burning, and other factors are favorable, excellent stands of seeded grasses may be secured.

This tendency of big sagebrush to repel invasion by perennial grasses gives rise to speculation concerning the nature of the relationship between established sagebrush and the seedling grasses. Although a brush cover of normal density doubtless intercepts and dissipates considerable rain and snow, competition for soil moisture is believed to be of paramount importance. Even so, complete removal of the brush prior to reseeding cannot be unqualifiedly recommended because of the known benefits of this type of cover in reducing insolation, runoff, wind and water erosion, and loss of snow. A method of reseeding which will reduce competition for moisture while preserving a portion of the cover is therefore desirable.

Scarifying the soil with a road ripper or chisel will prune sagebrush roots effectively to a depth of 9 to 12 inches at a reasonable cost. If the sagebrush is unable to regenerate roots and reoccupy this soil mass before grasses can become established, the use of such a machine may provide a biologically sound means of preparation for planting in dense sagebrush.

With these considerations in mind and in order to study the root regeneration habits of sagebrush, two trenches 2 feet wide and 10 feet long were dug in late August, 1940, to a depth of 2 feet approximately one-fourth mile apart in big sagebrush type near Wells, Nevada. The sagebrush plants were 35 to 40 inches tall and formed a moderately open stand with an understory mainly of *Bromus tectorum*. Severed ends of the brush roots on the trench walls were charted and found to have a weak tendency toward concentration above a depth of 15 inches. A typical square foot of trench wall contained 5 and 12 root ends in the two trenches, respectively. The soil was removed by horizons and after rocks and roots were taken out, it was tamped back into the trench in its former position.

In mid-November, following 10 weeks of abnormally high precipitation, one-fourth of each trench was carefully re-excavated. The soil was very moist to a depth of 7 to 8 inches, but no roots of sagebrush had re-entered the filled trenches.

Re-excavation of the second 2½-foot section on May 10, 1941, again revealed no regrowth of sagebrush roots, although perennial grasses had enjoyed 5 to 6 weeks of growing weather since the spring snow melt.

At the third examination three months later (August 8 and 11, 1941) numerous sage roots had developed and were occupying the soil rather

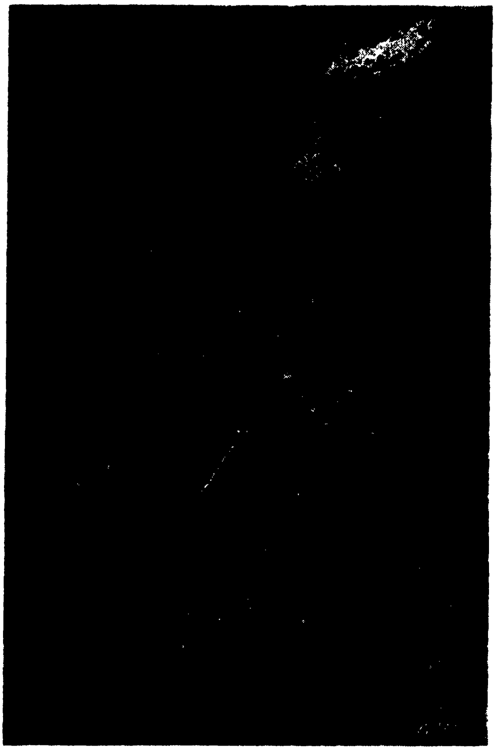

FIG. 1. Re-excavation of a trench 2 feet deep dug in sagebrush vegetation type in late August, 1940. None of these roots were present in May, 1941. Photographed August 11, 1941 (U. S. Forest Service photo).

fully (figure 1). The soil that had been returned to the trench at the previous (May) examination was ramified also by new roots from the trench walls.

After preliminary examination in both trenches had showed that the habit of the newly developed roots was similar in each, the roots from a 2-foot section (8 cu. ft.) of one trench were carefully isolated. Seventy-five roots ranging in length from 3 to 38 inches, with an average of approximately 12 inches, had reentered this mass of soil. Two-thirds of the total number were in the 7 to 12 inch soil layer.

The largest roots were one-twelfth inch in diameter. Secondary branches were profuse, ranging up to 7 per inch, and up to 10 inches in length. None of the small vertical branches extended nearer to the surface than 3 inches.

This evidence indicates that the active root growth of sagebrush occurs between May and August and coincides with, or slightly precedes, the period of most active shoot growth. Perennial grasses become semi-dormant during this period, having made most of their growth during the cool, moist weather of fall and spring.

This difference in periods of growth suggests that fall pruning of roots of sagebrush may provide an advantage for fall-planted grasses. Early fall pruning may be expected to increase fall storage of soil moisture and promote establishment of grass seedlings. The delay in regeneration of the brush roots the following spring may alleviate competition for soil moisture sufficiently during critical periods to foster establishment of the artificially reseeded grasses.

Although there is a need for machinery better adapted for the purpose, power-driven and horse-drawn scarifiers or rippers, penetrating the ground 9 to 12 inches, have been used experimentally as a means of seedbed preparation prior to broadcast seeding in sagebrush range depleted of its forage. Good stands have resulted from most of such plantings.

Studies to test the efficacy of superficial pruning of sagebrush roots are being continued in Nevada.

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BOOK REVIEWS

LEVELS OF INTEGRATION IN BIOLOGICAL AND SOCIAL SYSTEMS [1]

The eleven papers published in this volume of Biological Symposia were presented on the occasion of the celebration of the fiftieth anniversary of the University of Chicago. Representatives of the Division of Social Sciences of the University planned a program with the essential idea of presenting human society as an example of societies as a class and of examining some of the resemblances and differences among examples of the class. Meanwhile, biologists at the University projected a program of papers concerned with the ways in which, throughout the range of life-forms, parts are organized into wholes. It was recognized that the integration of parts into wholes within an organism and the integration of parts into wholes within a population or social aggregation, are not entirely separate problems, and that they could be considered in relation to each other and together. And so indeed they were through the combined efforts of the biologists and sociologists.

The papers fall into three groups, of which the first deals with the integration of the organism. The subject of Libbie H. Hyman's paper "The Transition from the Unicellular to the Multicellular Individual" is clear from the title. "Intermediate Levels of Organismic Integration" by J. William Buchanan, summarizes current ideas regarding the establishment of dominance by one part over the whole in the developing metazoan. "Higher Levels of Integration" by R. W. Gerard, discusses the development of transmission systems. These papers do not deal with problems of interest to the ecologist *as such* except through the analogies between the organization of individuals and of society.

The second group of papers is concerned primarily with relationships between organisms at a level of integration which is not characterized by a high order of social complexity. These are: "Synergistic Aspects of Bacterial Populations" by William Barrows; "The Transition from the Individual to the Social Level" by H. S. Jennings; "Integration of Infra-Social Insect Populations" by Thomas Park; and "Social Dominance and Subordination among Vertebrates" by W. C. Allee. The degree of social integration here at issue is that most commonly encountered in common ecological situations and this series of essays will be of most interest to the ecologist.

The third group of papers makes the transition from the higher orders of non-human social integration to that of modern man. The contributions are: "Basic Comparisons of Human and Insect Societies" by Alfred E. Emerson, "Societies of Monkeys and Apes" by C. R. Carpenter, "The Societies of Primitive Man" by A. L. Kroeber, and "Modern Society" by Robert E. Park.

It is an unfortunate attribute of symposia that integration takes place in the planning rather than in the performance. Once assembled, the participants standing on well planned common ground, have a way of shooting in different directions with unerring accuracy. So it is in the present case. The editor, Robert Redfield, admits in the Introduction that the great diversity among the papers may make it difficult for a reader at once to recognize their unity. They are all concerned with one aspect or another of the question, How are parts constituted into wholes throughout the range of life-forms? Nevertheless they are far from a systematic consideration of the problem. The general thesis developed may well be expressed in the words of the editor:

> "What these papers seem to be saying, in most general terms, is this: The organism and the society are not merely analogues; they are varieties of something more general: the disposition, in many places in the history of life, for entities to undergo such modification of function and such adjustment to other similar entities as result in the development and persistence of larger entities inclusive of the smaller. 'Fitness may mean cooperation for mutual benefit both between species and within integrated intraspecific populations as well as between parts of the organism.' Departing from the language of science, one might say that the individual metazoan, the infusorian population, the ant colony, the flock of fowl, the tribe, and the world-economy, are all examplifications of nature's grand strategy."

ALFRED C. REDFIELD

HARVARD UNIVERSITY AND
WOODS HOLE
OCEANOGRAPHIC INSTITUTION

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[1] **Redfield, Robert** (editor). 1942. Levels of integration in biological and social systems. Biological Symposia viii. Lancaster: The Jacques Cattell Press. Pp. 240. $2.50.

THE VERTEBRATE EYE [1]

The avowed aim of this book is that it should be entirely clear "to any college student or graduate, and to any amateur naturalist—'trained' or not." We may judge later how well it succeeds in its object.

The book synthesizes in an easily read style the enormous literature devoted to the comparative biology and evolution of the vertebrate eye. It is beyond question much more than a mere synthesis, since the author himself has made extensive contributions to the knowledge of comparative ophthalmology. Were not his whole-hearted immersion in the subject apparent on almost every page, that intensive interest would be evident to all who realize that this, like the other books by the same press, was published by invitation at no profit to author or publisher—truly a labor of love.

One's fear that this might be another work in pure or abstract morphology is quickly alleviated. Morphology occupies a deservedly important place, but the author never forgets that the eye is not an isolated organ which leads an independent existence. It is rather always described in terms of its functioning in the animal and in relation to the "seeing" conditions of the organism. Emphasis is placed on the functioning of the eye as a dioptric instrument and the functional and correlated anatomical changes which have accompanied the slow changes in habitat. Although the work is not intended to be encyclopedic in scope, the interested reader will find here the answers to questions which days of library work might fail to give. He will also find questions—and answers—which never before occurred to him.

The book is divided into three major parts which necessarily overlap in details. Each part is well-organized and logically developed. Part I—Basic—gives the minimal background material for understanding the rest of the book. There is a brief discussion of photoreceptors in general followed by a lucid description of the anatomy of the eye based on the human eye as a type. In connection with this basic anatomical description the properties of lenses are discussed. The usual subject matter is introduced (refraction, refractive errors, action of cornea and lens, etc.) in a fresh and clear manner. Following the description of retinal histology, the author leads the reader into the subject of rods and cones and their form-variety (long, short, double, twin and so on). Dr. Walls regards rods and cones as homologous cells which have evolutionary interchangeability. The compromise between the demands for sensitivity (mediated by the rods and summated by multiple nervous connections) and for visual acuity (served by the cones, with little or no summation) is brought out. Some eyes have gone entirely in one or the other direction, but many which must be active both in the light and the dark have both rods and cones and have modified the size of pupil and eyeball in "attempts" to achieve the best functional balance. Color vision is treated from a broad biological viewpoint in pleasing contrast to the usual limited discussion of human color vision alone. Color perception is a secondary acquisition of the cones and probably adds appreciably to their effectiveness as mediators of visual acuity.

There is a brief account of the embryology of the eye and a rather extensive account of the various theories of eye and lens origin in the pre-vertebrates. In discussing two of the proposed hypotheses of lens origin (the placode theory and Franz' theory) the author states that they stand or fall "with the demonstrability of a self-differentiating lens anlage." That the lenses in some amphibia are self-differentiating was discovered long ago by Spemann and confirmed by von Ubisch and Harrison. Thus, we need not await the day when the "juggleries (of the embryologist) may disclose that in some species of fish or amphibian a lens will start to develop without the presence of an optic vesicle."

The basic section concludes with a brief account of the phylogeny of the vertebrates.

Part II—Ecologic—deals much more extensively with many of the problems introduced in the preceding section. The visual modifications in animals of diurnal, crepuscular, nocturnal and twenty-four hour habit are taken up in detail. The methods of control of the amount of light and the quality of the image are discussed in relation to a wide variety of animals. The quantity of light reaching the visual cells may be controlled by photomechanical changes (migration of retinal pigment and simultaneous shortening of cones and lengthening of rods or vice versa). The quality of the image is controlled not only by the cornea and lens and the abundance of the photo-sensitive cells, but also by the production of intra-ocular color filters (macula lutea, oil droplets in cones, yellow lenses, retinal capillaries) which act to screen out short waves and increase acuity. Here again the specially developed areas of the retina receive attention, the area centralia and the blind spots which vary in shape in relation to the ocular habits. The significance of slit pupils and those of numerous other non-circular shapes are discussed along with the special function of the tapetum lucidum—a general name for reflecting layers which have been independently and nonhomologously developed in nocturnal and some twenty-four hour forms.

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[1] **Walls, Gordon Lynn.** 1942. The vertebrate eye and its adaptive radiation. Cranbrook Institute of Science. Bulletin No. 19. xiv + 785 pp.

The author devotes over one hundred pages to the anatomy and physiology of accommodation, the phylogenetic shifting of the lens, the possible rôle of the pecten in birds, visual fields (which attain near sphericity in some fishes) and the various anatomical and physiological dodges developed to detect movement. Here also binocular vision receives an interpretation far different from that of the text-books. Briefly, Dr. Walls regards overlapping monocular fields as binocular regions. The partial decussation of the optic nerves in mammals is interpreted not as a *sine qua non* for binocular vision, but rather as a mechanism for insuring conjugate eye movements with the resulting fixation of images on corresponding parts of the retina.

Color vision is broadly discussed in this section again and especially in relation to the external world. There is a broad account of skin pigmentation and color change here and its significance as a protective device. All too often, color significance has been judged in relation to the human eye rather than in relation to the historically more ordinary predators. In the final chapter the significance of special external coloration of the eye itself in relation to the skin coloration and concealment of the eye is extensively treated.

The final section, Part III—Synoptic—charterizes the eyes of each of the major vertebrate groups in terms of the eye as a whole and the special features found in retina, lens and so on. Much of the material of the two preceding sections is necessarily repeated here, but evolutionary aspects are particularly emphasized. Among other interesting conclusions we learn that the "sun-loving" snakes came from ancestors who went almost too far in adaptation to dim light and that the higher primates, including man, are descendants of nocturnal forms. This section will, of course, be of great value to those interested in particular groups.

In general summary, we may attempt to state an answer to the opening question: How well does it succeed in its object? Part I could be read by anyone with elementary knowledge of biology. Parts II and III, however, despite their clarity, bring in many specific and generic names which offer difficulty to anyone not well-versed in vertebrate taxonomy. These would discourage such a hypothetical reader without perhaps driving him away. Certainly for any naturalist, biologist or physician interested in the eye this is a splendid work. It is equally valuable to an ecologist interested in special behavior problems in which visual cues predominate.

The book is attractively printed and put together. The illustrations are exceptionally clear, carefully worked out and sufficiently abundant, there being probably about six-hundred separate drawings in 197 figures. There are eleven summarizing tables of great survey value, a selected bibliography and an index-glossary.

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AN ECOLOGICAL APPROACH TO ENTOMOLOGY [1]

In the preface to his book, Professor Frost sets forth certain limited objectives. In general these are (1) the book is written for classes in elementary college entomology; (2) the text is general in nature and attempts to cover all phases of the subject; (3) taxonomy, physiology, morphology and economic entomology are minimized since there are other excellent books dealing with these aspects; (4) since there has been a great advance in knowledge concerning the classification and ecology of insects, and since courses in entomology are often given during the winter, the ecology of insects is emphasized.

It would be unethical to criticize the book beyond the scope of the author's objectives and therefore I should like to say now that these objectives have been met with creditable success, and that my criticism is not of the book so much as the situation which made the limitations necessary.

It is a pleasure to have a text designed for elementary college entomology. Having used the book for two classes in elementary entomology I am convinced that it is not large enough. If it were twice as large the aspects minimized could have been included. Entomology is not taught enough in the United States. Most college students receive their bachelor degree with no realistic appraisal of insects. They are ignorant of the grim struggle for control of the environment, of the rôle insects play in agriculture, the insects as vectors of disease, the light entomology has shed upon the study of inheritance, and many other contributions to our civilization. From this viewpoint the part of the text dealing with anatomy, and especially physiology should have been expanded. The reviewer should have liked a summary of modern physiological research after each section of comparative anatomy, and especially our advance in the study of insect endocrinology. Histology of insects is seldom adequately treated in entomology; embryology usually summarily dismissed; almost always no section on genetics. This last is particularly odd since the insects have played a major part in the research of modern genetics and students seldom appreciate the importance of insects in this field. In summing up this portion of the book, then, we feel that the subjects minimized should have been extended, and genetics added, since the book is intended for students, most of whom will not pursue entomology as a profession.

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[1] **Frost, S. W.** 1942. General entomology. New York: McGraw-Hill. x + 524 pp. 406 figs. $4.00.

The fourth, and principal objective of the book, namely the ecology of insects, is well written and of interest to students taking their first course in entomology. It makes available much species ecology, conveniently summarized, and is especially valuable if these students can combine their course in entomology with a course in Field Zoölogy where spot analyses of amphibian and bird stomachs can be combined with rough quantitative population assays of the community under study. I found Chapters XVI to XXII well presented.

Technical literature is gathered at the end of each chapter and these citations are in general well selected. We note in passing that the important work of Isely on background coloration and predation of grasshoppers is not listed in the bibliography of Chapter IX, and the research of the past ten years on insect activity pattern is not given the place some feel it deserves.

Some errors have crept past the proofing of the book and while this is inevitable, three deserve mention. On page 22 in the upper table, the species of hesperoid and papilionoid Lepidoptera in the Neotropical area are totaled as 4,743 but the column adds up to 5,743 species. On pages 95 to 98 a good key to orders of insects is marred by four incorrect citations to the accompanying illustrations of key characters. On page 276, the legend of figure 217 is incorrect. It is stated that "another species of *Necrophorus*" is below. The beetle referred to is not *Necrophorus*, but a species of *Silpha*, probably *Silpha surinamensis*. These, and more minor slips, can be easily corrected by the instructor and the reviewer mentions them solely for this purpose since he is well aware of numerous slips in the proof-reading of his own papers.

There is a workable index to the book, but no glossary.

It is to be hoped that Professor Frost will enlarge his book since it is worthy of attention and its ecological approach should fill a genuine niche in the teaching of the subject.

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A MONOGRAPH ON COPEPODS[1]

All interested in copepods or the plankton have long been indebted to the late Professor Charles Branch Wilson, lately Professor of Biology Emeritus, Massachusetts State Teachers College, Westfield, Mass. His comprehensive knowledge of copepods, unflagging industry, meticulous accuracy and conservative judgment have enabled him to produce monographs of high distinction, even during the years since he passed the milestone of three-score-and-ten, and before his death last year. The Carnegie report, to quote Dr. Waldo Schmitt, "perhaps the most important in Dr. Wilson's own opinion, deals with the copepods of the marine plankton taken on the last cruise of the ill-fated non-magnetic yacht Carnegie. This report, which was submitted for publication several years ago, for the first time in the history of oceanography gives the directly comparable results of simultaneous three-level tows made in all oceans with identical gear, accompanied by full station data, including temperature, salinity, density, phosphates, and hydrogen-ion concentration. . . . Dr. Wilson has made available a biologic record of a group of organisms of highest importance in the economy of the seas such as has never been achieved by any marine expedition." Since copepods are undoubtedly the most numerous components of the animal plankton community (Russell, F. S., '34), this Carnegie report is of no little significance to general oceanography. These world-wide collections, so far as they were made at the *regular* stations, were all taken at about the middle of the forenoon, and this regularity of the time of the tows adds greatly to their value for purposes of comparison. Fortunately there were also surface tows between stations taken at other hours, but most often at night, thus supplying valuable data with reference to upward migrations of certain species during the night.

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[1] **Wilson, Charles B.** 1942. Copepods of the plankton gathered during the last cruise of the Carnegie. v + 237. 3 full page maps, 16 charts, 136 figures. Washington: Carnegie Institution. Publication 536. $3.50 (cloth); $2.50 (paper).

Wilson's publications are characteristically models of plan. In the first fourteen double-column pages there are given maps, an adequate account of apparatus and methods, a discussion of qualifying conditions and extended comments on comparisons between the two oceans and between the different regions of the Pacific and on distribution and stratification in relation to various conditions of the environment. The lists of species by stations occupies some 150 pages, following which are 42 pages with brief discussions for each species. There is a bibliography of more than 120 references, a list of species discussed, 136 very clear figures, a number of special small charts in the text and, finally, an index of species and synonyms. There is a preface by Dr. J. A. Fleming, Director of the Department of Terrestrial Magnetism, with an acknowledgment to Dr. Waldo L. Schmitt, Curator of the Division of Marine Invertebrates of the U. S. National Museum, and his associates for certain necessary additions to the manuscript and other aid in the editorial tasks incident to a posthumous publication.

When it is considered that there were 283 species, that studies were made for 160 stations, and that sometimes there were approximately 100 species at a station, it can be seen that a prodigious amount of work by the author was involved.

For the parts covered by the Cruise, the Pacific was much richer in species than the Atlantic ocean, there being identified 265 species in the Pacific as contrasted with somewhat less than half that number (132) in the Atlantic collections. No Atlantic station yielded more than 60 species but 32 Pacific stations returned 71 to 108 species. Wilson emphasizes the fact that this is only a partial comparison between the oceans, but he believes that more extensive coverage would not be likely to bring the Atlantic up to the Pacific in number of species of copepods. On the other hand, there were encountered no great aggregations of copepods in the Pacific such as occurs with *Calanus finmarchicus* in the North Atlantic. As has been reported before, tropical waters are much more prolific in numbers of species, but distinctly less so in volume. This general phenomenon is illustrated by the fact that for 12 stations north of 40° lat. there was an average of 16 species, while for 10 stations in the tropics there was an average of 83 species.

Under the heading of "Diversity of Distribution" he discusses irregularity of distribution in the plankton and suggests that "even in restricted areas, what may be termed the 'personnel' of the plankton is constantly changing. Two tows over the same area, no matter how quickly one may follow the other, will never yield identical results." Thus, when two tows were made consecutively at the same locality on the same day and with the same net, more than half (23) of the 43 species taken were found in one tow only; and the illustration is not unique.

Many data regarding daytime stratification were found and "almost every species in each of the station lists show some degree of preference as to depth." In a discussion of the causes of daytime stratification, Wilson is inclined to dismiss temperature as an insignificant influence. He assumes that a difference of two or three degrees in temperature at different depths could not be effective and also that concentration of copepods should be positively rather than negatively correlated with height of temperature. With characteristic fair-mindedness he adds, after a discussion of certain tropical areas, that "These variations are all of sufficient magnitude to suggest an appreciable influence of temperature on stratification. An examination of the species lists at these stations reveals exceptionally well marked stratification, but in every instance it is the exact opposite of what it should be, on the hypothesis that higher temperature induces greater concentration of copepods." It occurs to the reviewer that, if the hypothesis were reversed, the influence of temperature on stratification would be supported by all of the evidence presented. His argument is summarized in the statement: "We are forced to conclude, therefore, that in most cases the temperature variation is not large enough to produce the amount of stratification shown; and when it does appear to be of sufficient size, it seems to have the opposite effect from what would be expected."

Naturally, certain species of copepods are found to be widely tolerant of temperature, occurring at 200 meters where the temperature was below 3° and in the upper 100 meters where the temperature was from 15 to 21°.

Salinity, density and hydrogen ion concentration seem to have no appreciable influence on vertical distribution. Sunlight is left as the probably critical environmental factor causing daytime stratification. Wilson discusses this at length along with the evidence adduced by various investigators on diurnal migration. He concludes that, since more species should be obtained at night in the surface waters, the "Carnegie towings" probably did not obtain all the species that occur within the upper 100 meter waters. His final comment in that discussion, as a general suggestion for future surveys, may be quoted: "A surface towing in the night, on the contrary, might give a very respectable indication of the total plankton, since many of the species that remain at deeper levels during the daytime come to the surface at night. To obtain satisfactory results, therefore, there must be tows at different levels during the daytime and these must be supplemented by tows at or near the surface at night."

Wilson's Carnegie report is a fitting climax to a long life in service to science, effective teaching and personal and scholarly integrity. The Carnegie Institution of Washington is to be congratulated upon the general quality and the excellent format and typography of this first biological monograph in the series of "Scientific Results of Cruise VII of the Carnegie during 1928–29 under the command of Captain J. P. Ault."

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Taxonomy and Ecology of Pselaphid Beetles [1]

This book is a pioneer taxonomic study on a poorly known family of beetles. It undoubtedly lays the foundation for future biological work on these insects. Species of the family are principally found in plant debris and vegetable mold and in the nests of ants and termites. They are primarily nocturnal in their activity and are more abundant in the tropical regions. Pselaphids are mostly predacious. The myrmecocoles, however, may be fed with regurgitated food by the host ants. Some myrmecocoles have highly modified glandular trichomes which serve to integrate the beetles with their host ants. The more restricted the host relationship, the more specialized is the structure of the beetle.

In spite of admittedly inadequate data, Park attempts interesting zoögeographical analyses on faunal origins, highways of distribution, altitudinal effects, and taxonomic density. Special emphasis is given to the faunal and ecological relations of the Pselaphids of Barro Colorado Island in the Canal Zone where intensive studies were undertaken. The number of described neotropical species is 895. Park estimates that 7000 to 14,000 species exist in the neotropical region which may have a population of 651,000,000 individuals with a biomass of 2,604 kilograms and an average of 46,500 individuals in each species population. These figures are highly speculative.

The book is valuable to the ecologist in showing the relationship between ecology and taxonomy and in demonstrating the enormous gaps in our knowledge of species ecology, particularly among the insects of the rich tropical faunas. It is the reviewer's opinion that much more accurate ecological work would be done if ecologists were more often interested in taxonomy and taxonomists were more often interested in ecology.

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University of Chicago

American Wildlife [2]

Fading Trails presents an interesting and authentic account of the various ways in which the march of man across the North American continent has brought about the complete, or nearly complete, extermination of many forms of wild life that flourished in the early pioneer days. Uncontrolled exploitation of natural resources and the instinct to kill anything that moved across land or water led not only to direct destruction of vast numbers of animals but brought about depletion of many species indirectly though just as certainly. While examples of direct extermination, such as those of the passenger pigeon, the sea otter, and the buffalo are familiar to all, the more remote effects of man's rapacious activities are less well recognized. Among numerous examples of the latter effect which the authors cite may be mentioned that of the rapidly approaching extinction of the ivory billed woodpecker resulting from the destruction of forests. This bird depends for its food on beetle larvae which feed between the bark and sapwood of large dead trees. Since these larvae can obtain sustenance from this locus for only two years after the death of the tree the food supply of the woodpecker is limited. Cutting down the forest deprives the ivory bill of its only source of food.

Considerable attention is given to the ecological problems involved in the perpetuation of certain species of birds and mammals which adds much to the value of the book. One of the most interesting chapters is that on the life in the Everglades. In the days before canals and roads were driven through the Everglades an abundant and most varied wild life existed in this extensive and completely isolated region of Florida. While the food supply was abundant the relationships between food and population density of many species was most delicately adjusted. An instance of this ecological balance is that of the snail bird—a kite—whose sole source of food is a large fresh water snail. When canals 6–10 feet deep were dug through this country the water level was lowered, the glades dried up and the snails together with innumerable other foods of bird and mammal vanished.

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[1] **Park, Orlando.** 1942. A Study in Neotropical Pselaphidae. Evanston, Ill.: Northwestern Univ. Studies Biol. Sci. and Med. No. 1, x + 407 pp., xxi pl. $7.50.

[2] **Beard, D. B., F. C. Lincoln, V. H. Cahalane, H. H. T. Jackson and B. H. Thompson.** 1942. Fading Trails. N. Y.: Macmillan Co. $3.00.

In so far as justice can be given to man in this respect it is pointed out that not all the forces bringing about extinction of wild life are attributable to human agency. An example of the deleterious effect of certain natural changes is afforded by the diminution in numbers of the roseate spoon bill, as a result of the growth of mangroves which have progressively linked up land masses, thus removing islands on which the spoon bills nested. Connection with the land, made their nests accessible to certain egg-eating predators, particularly racoons and rats.

While the joint authorship of this book has certain definite advantages in that it has brought together special knowledge in a number of entirely diverse fields it has also the disadvantage of being unevenly written. Some chapters are much better than others. This is illustrated by the two chapters on the mountain lion and the wolf. The chapter on the wolf is so well written that, in spite of this animal's unsavory reputation, you are made to feel that such an interesting species should be preserved from extinction. On the other hand the treatment of the mountain lion is such that on finishing the account one is left with little interest as to whether this animal survives or disappears. Again there is a repetitious and trite quality to certain parts of the opening chapters which may well discourage some readers from proceeding to the more interesting sections of the book.

These shortcomings in no way detract from the value of this presentation as a whole. Within the short space of 264 pages is brought together a remarkable collection of reliable data on a number of animal species past and present, together with information as to what is now being done to restore the fading trails.

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Department of Medicine,
University of Chicago

Bennett, Hugh Hammond and William Clayton Pryor. 1942. This land we defend. xii + 107 pp., 19 photogravures, 2 maps. Longmans, Green and Co., New York. $1.50. The story of soil impoverishing and disregard of measures for soil conservation in the United States during the past three hundred years. What has been done more recently and what remains to be done for soil enrichment and conservation. A timely book not only for farmers but for every American.—C. S. G.

Waksman, Selman A. 1942. The peats of New Jersey and their utilization. Part A. 155 pages; 18 illustrations. Trenton, N. J. Department of Conservation and Development, State of New Jersey. Bull. 55. Geologic Series. This bulletin deals with the nature and origin of peat, its composition and utilization. The scope of the work is indicated by the title headings, as follows: The nature of peat, its formation and abundance; Terminology of peat and causes of confusion; Types of peat and systems of classification; Climatological, geological, and botanical factors involved in peat formation; Chemical composition of peats; Physical and physico-chemical properties of peat and peat soils; Microbiology of peats; Utilization of peat for agricultural purposes; Industrial utilization of peat. Bibliography of 339 titles.—C. S. G.

ECOLOGY

VOL. 24 APRIL, 1943 No. 2

ON THE ESTABLISHMENT AND GROWTH OF CERTAIN LEGUMES ON ERODED AND UNERODED SITES[1]

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INTRODUCTION

In a recent investigation (Drew, '42) of the revegetation of abandoned cropland in Boone and Callaway Counties, Missouri, attention was called to the frequent occurrence of various legumes in eroded old fields. As an outgrowth of these observations, the present study is an attempt to determine differences in the establishment and growth of several species of legumes on eroded areas of a given soil type[2] and to evaluate some of the edaphic factors related to these differences. Two native legumes, *Cassia fasciculata* Michx., an annual, and *Lespedeza virginica* (L.) Britt., a perennial, both frequently found in eroded old fields, were selected along with two introduced legumes, *Lespedeza stipulacea* Maxim., an annual, and *L. sericea* Benth., a perennial, for the experimentation. *L. stipulacea* at present is widely planted in this area as a cover and forage plant on poor soils, and *L. sericea* is being used increasingly for the same purpose. The two particular species of native legumes were selected principally because of an adequate supply of excellent nursery-grown seed furnished by the Soil Conservation Service nursery at Elsberry, Missouri.

It was hoped that the study would indicate: (1) the effect of the various chemical and physical factors of the soil which are changed by erosion, upon the establishment, growth, and composition of these legumes; (2) the relative value of the legumes as to their ability to compete with other vegetation under adverse conditions; (3) their relative value as producers of soil cover; and (4) their relative value as efficient users of soils of low nutrient levels and poor physical conditions.

Except for a recent paper by Allard ('42), who has evaluated soil factors responsible for the dearth of natural vegetation in certain bare areas of old fields on Bull Run Mountain, Virginia, very few ecologists have attacked directly the problem of the factors involved in the diminution of growth of plants on eroded or very poor soils. However, closely related aspects of this

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[1] The writers wish to acknowledge gratefully the assistance rendered them during this investigation by the following persons: Mr. H. A. Steavenson and Mr. C. J. Coukos of the U. S. Soil Conservation Service, for suggestions and generous contribution of materials; Professor C. A. Helm, Department of Field Crops, for seed of *Lespedeza stipulacea;* Mr. D. E. Wade of the University of Missouri Wildlife Area and Arboretum, for his excellent cooperation in facilitating the study; Dr. W. A. Albrecht and Dr. E. R. Graham, of the Soils Department, for most helpful criticism and suggestions in connection with soils analyses; and members of the Botany Department who have aided in the field work and have offered valuable suggestions.

[2] Although the soil type (Union silt loam) on which these studies were conducted differs in various respects from those (Lindley series) on which the revegetation process was investigated, observations, repeatedly verified, indicate little substantial difference in this general area in the vegetation on these two soil types.

problem have been studied by numerous investigators in the general fields of water relationships and mineral nutrition of plants in the soil. A detailed review of the literature will not be given here, but pertinent papers are referred to in the discussion of results.

EXPERIMENTAL METHODS

Field plots

The area upon which the present work was done is in the University of Missouri Arboretum and Wildlife Conservation Area four miles east of Ashland, Missouri. The topsoil from several hundred square rods had been removed rather uniformly from a ridge top for use in the building of a nearby road. An adjacent area had been untouched since the field was last cultivated. Eight-year-old sassafras sprouts indicated that the field had been abandoned approximately eight to ten years ago and it was supporting a mid-seral stage in old-field succession (*cf.* Drew, '42). *Solidago nemoralis*, *Aristida oligantha*, and *Aristida longespica* were very abundant; *Panicum capillare* was abundant; and *Cassia fasciculata*, *Apocynum cannabinum*, and *Aster pilosus* were common.

The soil profile consists of an A horizon about six inches deep of a light brown color, silt loam in texture, pulverizing finely between the fingers. The B horizon is a lighter yellow-brown, heavier in texture, and grades gradually into a heavier clay, which remains friable and well drained. The soil is of loessial origin—typical Union silt loam.

On the "eroded" area the entire A horizon had been evenly removed leaving the subsoil exposed. This area after three years supported a very sparse vegetation consisting of typical poor-soil grasses and some annual legumes. Considerably less than half the ground was covered at any time of year. *Setaria lutescens*, *Aristida oligantha*, and *Aristida longespica* were very abundant; *Cassia fasciculata* and *Strophostyles helvola* were abundant; and *Solanum carolinense* and *Solidago nemoralis* were common.

An area 150 by 100 feet was laid out so that one half was on the "eroded" part and one half on the "uneroded." Sixteen plots were marked off for four replications each of the four legumes selected. The soil was double-disced and the seed planted (April 2, 1941) with a three-foot drill uniformly across both eroded and uneroded parts. Although the *Cassia fasciculata* seedlings and a few lespedezas had appeared within ten days after planting, three subsequent torrential rains flattened out the drill ridges and completely covered the germinating seedlings of all three species of lespedeza. Accordingly these three species were replanted with a hand drill on May 20.

During June and July one-half of each plot was weeded in order to determine the effect of competition both upon differences among species and upon differences between the two areas. Count-weight quadrats were used to measure differences in Cassia and *Lespedeza stipulacea*. Permanent count-list quadrats were set up one to each plot of the perennial lespedezas. Total populations of both weeds and planted species were recorded during October, 1941, and again during April and June of the following year.

Complete tests were made of both soils. Exchangeable calcium, magnesium, and potassium were determined by spectroscopic analysis of ammonium chloride leachate of soil. Total hydrogen and pH were determined potentiometrically, and total exchange capacity by distillation of ammonium chloride-leached samples. Percentage of carbon was determined by the oxygen-combustion method, nitrogen by the Kjeldahl technique, and phosphorus by the molybdate colorimetric quick test. Moisture equivalent was measured according to the method outlined by Briggs and McLane ('07, '10), and wilting coefficient by the method of Briggs and Shantz

('12). Moisture content of the upper three inches of soil was determined at approximately two-week intervals during the summer.

Greenhouse cultures

The second phase of the investigation consisted of pot cultures of both soils brought into the greenhouse, given various treatments of calcium, phosphorus, and potassium and planted to *Lespedeza stipulacea*. Three-gallon stone jars were filled with soil in the field, the profile being kept as nearly normal as possible. Then the top six inches from each pot was removed, weighed, and mixed with an exact amount of fertilizer. Calcium was applied as $CaCO_3$, potassium as K_2CO_3, and phosphorus as $CaHPO_4$. Four replications were made of each treatment on both eroded and uneroded soils. In each case treatment was applied to only the top six inches.

The treatments given the soils are outlined below. (1) A series in which calcium was added up to saturation of the exchange capacity, in order to determine the relationship of calcium to the differences in growth. (2) A series in which the potassium supply was doubled and calcium added to saturation in order to eliminate the possible influence of low potassium on the reaction of the plants to low calcium. (3) A series in which calcium was brought up to saturation and a basic application of 0.1 milligram equivalent of phosphorus was added per 100 grams of soil, in order to check the possibility of phosphorus deficiency. (4) A series with only the basic application of phosphorus. (5) Control pots handled in an identical manner except that no nutrients were added.

Seeds were planted on April 23,[3] and as soon as the seedlings were well established they were thinned to 30 plants per pot. Only distilled water was added in order to maintain the nutrient balance. The soil was kept as nearly as possible at optimum water content at all times in order to eliminate water availability as a factor in growth. On June 20 the plants were moved out of doors to escape red spider.

On July 20 the plants were harvested and dry weights of both roots and tops grown in each pot were obtained. Tops from each series were ground in a Wiley mill, mixed thoroughly, weighed oven-dry, and dry-ashed. Determinations were made of calcium, magnesium, and potassium content by spectroscopic analysis (accurate to within 5 per cent of amount present). Total nitrogen was determined by the Kjeldahl technique as modified by Murneek and Heinze ('37), and phosphorus by the colorimetric method outlined by Snell ('36), using stannous chloride reduction of the phospho-molybdate.

No nitrogen treatments were given in the first set, since it had been suggested (Ferguson and Albrecht, '41) that legumes can utilize nitrogen fixed by their own nitrogen-fixing bacteria. All three species of lespedeza used belong in the same group with respect to the strain of nitrogen-fixing bacteria which they support (Bushnell and Sarles, '37). Moreover, the soil was already inoculated in the field by the presence of well-nodulated wild *Cassia fasciculata* and *Strophostyles helvola*, which are also in the same group as the three lespedezas. However, in 1942, a second set of cultures was grown in which nitrogen alone was added to one series, and to one series in conjunction with other nutrients. In this second set, half-calcium saturation was given to some series in order to check the possibility of calcium toxicity to lespedeza when at complete saturation.

Plants of the 1942 experiments were grown in six-inch pots with three plants to each pot. All the soil was treated and five replications of each of the following treatments were made: (1)

---

[3] The pots containing uneroded soil with phosphorus added were planted June 2 and harvested August 5.

one-half calcium saturation; (2) calcium saturation; (3) one-half calcium saturation plus 0.1 milligram equivalent of phosphorus per 100 grams of soil; (4) calcium saturation plus 0.1 milligram equivalent of phosphorus per 100 grams of soil; (5) calcium saturation plus 0.1 milligram equivalent of phosphorus per 100 grams soil plus doubling of the potassium content of the soil plus about 20 milligram equivalents of nitrogen per 100 grams of soil; (6) about 20 milligram equivalents of nitrogen per 100 grams of soil; and (7) controls given no treatment. This set of cultures was planted April 1 and was harvested and dry weights of the tops obtained on June 24.

Experimental Results

Results of soils analyses

Mechanical analysis of the two soils showed that the uneroded topsoil had 14.5 per cent clay of 0.005 millimeters diameter or smaller, while the eroded soil had 28 per cent. This fundamental difference was reflected in the total exchange capacity, which was nearly twice as much on the eroded as on the uneroded soil. The greater exchange capacity correlated almost exactly with the greater clay content. The data given in table I show, however, that available nutrients were not proportionately greater. Total calcium was only slightly higher in the eroded soil, so that the percentage calcium saturation was much lower. Potassium was actually lower, and both carbon and nitrogen, while very low in both, were slightly lower in the eroded soil. Only magnesium showed an increase proportionate with the increase in exchange capacity. The carbon-nitrogen ratio was low, but narrower in the uneroded soil, which indicated that the rate of bacterial activity and turnover of organic matter was very low on both soils, though somewhat higher on the uneroded than on the eroded soil. Phosphorus was also very low in both.

Table I. *Comparison of soils*

Soil factor	Uneroded soil	Eroded soil
Total exchange capacity	6.5 M.E.*	11.0 M.E.
Calcium	3.6 M.E.	4.0 M.E.
Total hydrogen	1.5 M.E.	4.0 M.E.
Potassium	0.375 M.E.	0.275 M.E.
Magnesium	1.0 M.E.	2.0 M.E.
Per cent Ca saturation	55.0%	36.0%
Per cent base saturation	76.0%	63.0%
pH	6.6	5.2
Per cent carbon	0.68%	0.5%
Per cent nitrogen	0.068%	0.045%
Carbon-nitrogen ratio	10.0	11.1
Organic matter	1.21%	0.89%
Per cent clay	14.5%	28.0%
Moisture equivalent	13.5%	18.5%
Wilting coefficient	5.2%	10.5%

* The abbreviation "M.E." stands for milligram equivalents.

The large difference in amount of hydrogen on the exchange complex was not reflected in the pH difference, which was relatively small. The larger exchange capacity of the eroded soil held a much larger amount of hydrogen as well as a somewhat larger total amount of exchangeable bases than the uneroded soil. Actually, then, nutrient cations were less readily available to the plant from the eroded soil, since the percentage saturation of these ions was smaller and the rest of the exchange capacity was taken up by hydrogen.

The structure of both soils was very poor. No stable aggregates were formed on the uneroded soil. Even a moderate rain smoothed and packed the surface. The eroded soil tended to form large compact grains, but these also were broken down upon prolonged wetting. The higher percentage of clay made it very sticky and it tended to form clods if worked when too wet. The water-retaining capacity of the eroded soil was considerably higher than the uneroded, as would be expected because of the larger percentage of clay. Moisture equivalent and wilting coefficient (table I) were both higher on the eroded soil.

Results on field plots

Quadrat counts made of *Cassia fasciculata* on July 3 and 9 showed that from nine quadrats taken at random in the unweeded portions, the eroded area had 121 plants per square meter, and the uneroded had 90. The growth was greener and heavier on the uneroded portion and the plants were 18 to 24 inches high as compared with 15 to 19 on the eroded soil. Cassia started growing so early, April 10, that weeds gave it little competition and weeding caused no observable difference in growth. On August 4, clip quadrats of one square meter were made. Averages of four quadrats were as follows:

Plot	Number of plants	Dry weight in grams
Uneroded weeded	102	185
Uneroded unweeded	110	202
Eroded weeded	135	150
Eroded unweeded	137	145

Numbers varied much more than weights from quadrat to quadrat within a group. Comparison of the numbers of plants per square meter on the two areas appear to indicate a greater percentage of survival on the eroded soil than on the uneroded, though the smaller number of plants on the uneroded soil produced more weight. Cassia bloomed during June and July, matured seed, and died during August. By mid-autumn, very little soil cover remained.

In order to check for *Lespedeza stipulacea* this possibility of differences in establishment of seedlings on the two soils, counts were made of fifty 20-centimeter strips taken at random along the drill rows of the weeded plots. On July 9, the average number of lespedeza plants per strip was 54 on the uneroded and 66 on the eroded soils. On August 1, these numbers had dropped to 34 on the uneroded and 60 on the eroded, and on September 13 to 34 and 48. The possibility seems greater that the lower numbers on the uneroded soil result from competition between the plants themselves rather than from a lower percentage of germination. Seed from the same source planted on the same soil type in the greenhouse gave practically 100 per cent germination on both eroded and uneroded soils. During the later counts, large numbers of dead plants of this species were found on both soils wherever the planting was thick and none where it happened to be thin. Larger growth on the uneroded soil caused more competition and fewer plants survived. The most severe competition among seedlings of *L. stipulacea* came early in the season when growth was rapid.

On October 1f, clip-quadrats were made of *Lespedeza stipulacea.* Growth was complete, seed had been matured, and the leaves were beginning to turn brown and fall off. Within two weeks the plants were all dead. The following dry weights per square meter were obtained as averages from four quadrats each:

Plot	Weight in grams
Uneroded weeded	202.9
Uneroded unweeded	89.2
Eroded weeded	131.2
Eroded unweeded	108.2

As the foregoing data indicate, *Lespedeza stipulacea* met weed competition much more successfully on the eroded area where the soil was poorer and conditions for weed growth not as good. Such a result compares favorably with the findings of Campbell ('27) who noted that legumes compete better with non-legumes on poorer soils. *L. stipulacea* produced a large amount of seed, and germination the following year was good. During the 1942 season both areas were covered by a thick stand, yet with evident differences in size and color of plants between eroded and uneroded sites.

Since *Lespedeza sericea* and *L. virginica* are perennials, they were difficult to measure adequately during the first year. Heights and sizes varied greatly among the various treatments. Judging by appearances the first year they met competition very poorly, partly, no doubt, because most of the growth was made after August 1. The average height in inches at the end of the season in 1941 was as follows:

Plot	*L. sericea*	*L. virginica*
Uneroded weeded	23.0	22.8
Uneroded unweeded	16.5	12.7
Eroded weeded	17.1	17.0
Eroded unweeded	9.5	9.0

Lespedeza virginica bloomed and set seed on the weeded plots on both soils. *L. sericea* did so on the uneroded, but not on the eroded site, though it produced as much vegetative growth as *L. virginica*. All the perennials remained green until the first killing frost November 20.

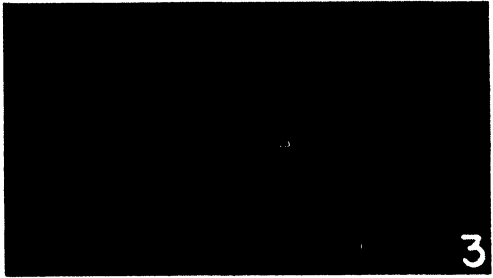
The root systems showed much greater uniformity among soils and treatments than the tops, though of course the size of the root system tended to vary with the size of the plant. The perennials had much larger root systems in proportion to the amount of tops than did the annuals. *L. virginica* had, under all conditions, a large taproot extending down into the soil from 18 to 24 inches or more, the length varying somewhat according to the size of the plant. In *L. sericea*, there were frequently two or three taproots which did not extend quite as deeply, but in other respects the root systems were very similar. Roots of all plants were well nodulated.

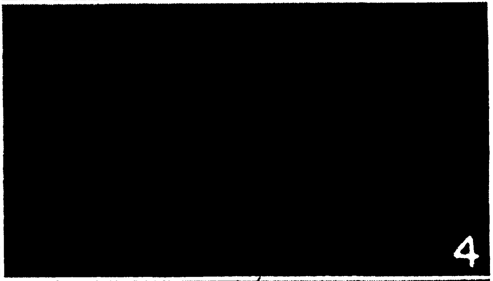
Permanent quadrats, one per plot of *Lespedeza sericea* and *L. virginica* were laid out and counted during October, 1941. Data are summarized in table II. These figures are averages from counts of eight or, in some cases, four quadrats. Both *L. sericea* and *L. virginica* decrease in numbers as competition increases, and were fewer on the eroded soil. The dominant weeds on the uneroded soil were *Panicum dichotomiflorum* and *Panicum capillare*. On the eroded site *P. capillare* was almost entirely absent and was replaced by *Setaria lutescens*. Several species of forbs occurred sparingly on both areas. The weeds showed the same differences as the planted legumes —more plants of smaller size occurred on the eroded soil. While an inspection of the data in table II might appear to indicate that in some of the plots there were as many weeds on the weeded as on the unweeded portions, actually those which occurred on the former were small seedlings which had germinated after weeding (June-July) had

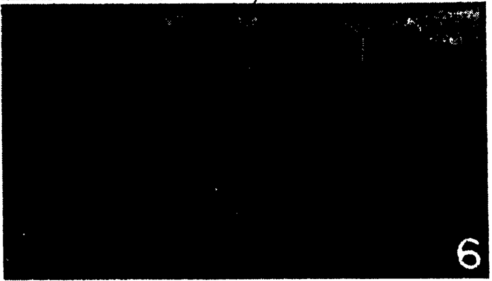
TABLE II. *Quadrat counts of plots of perennial lespedezas, October, 1941.*

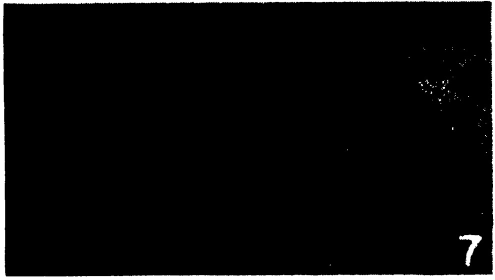
Name of plant	Average number of plants per square meter							
	L. sericea plots				*L. virginica* plots			
	Uneroded		Eroded		Uneroded		Eroded	
	Weed.	Unweed.	Weed.	Unweed.	Weed.	Unweed.	Weed.	Unweed.
Lespedeza sericea	277	189	199	116				
Lespedeza virginica					152	113	122	107
Forbs	1*	1*	1*	5	5	13	3	10
Grasses	13	41	51	204	9	34	38	190
Total average number of plants per square meter	291	231	251	325	166	160	163	307

* Average of one or less per square meter.









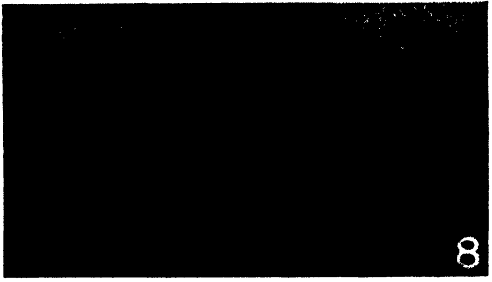


FIG. 1. *Lespedeza sericea* at end of first season on uneroded soil. FIG. 2. *L. virginica* at end of first season on uneroded soil. FIG. 3. *L. sericea* at end of first season on eroded soil. FIG. 4. *L. virginica* at end of first season on eroded soil. FIG. 5. *L. sericea* (left) and *L. virginica* (right) during second season on uneroded soil. FIG. 6. *L. virginica* during second season on eroded soil. Weed area to the left was *L. sericea* plot of the previous year. FIG. 7. *L. stipulacea* on uneroded soil during second year. FIG. 8. *L. stipulacea* on eroded soil during second year.

ceased. The grasses on the eroded soil all exhibited a reddening of the stems which was absent on those on uneroded soil. *L. stipulacea* showed this reddening, but to a lesser degree, both out-of-doors and in the greenhouse.

Counts were made of the permanent quadrats on April 25, 1942. *Lespedeza sericea* showed 31 per cent survival on the uneroded, weeded plots, and 68 per cent survival on the uneroded, unweeded plots. Less than a dozen living plants could be found on the eroded area. *L. virginica* had not grown enough to count accurately in April. A recheck on June 25 showed 90 per cent to 95 per cent survival of this legume on both eroded and uneroded, weeded and unweeded areas. Practically all of the *L. virginica* survived the winter, while *L. sericea* nearly all died on the eroded soil and one-third to one-half on the uneroded soil. The aspect of the plots the second season, as compared with the first season, is shown in figures 1–6. Frost-heaving was very severe on the eroded soil and in early spring two to four inches of the root system of many of the young plants of both species of perennials were exposed.

A somewhat different weed flora was found, of course, in April. *Veronica peregrina* and *Lepidium virginicum*, which were not found the previous year, occurred at an average of 35 plants per square meter and 4 per square meter respectively on the uneroded soil. In addition, scattered seedlings of several species of forbs were found, some of which had been noted the previous year. The most numerous grasses of the October counts, Panicum, Aristida, and Setaria, were coming up very thickly on all areas, and were one-fourth to one inch high. Wherever *Lespedeza stipulacea* had produced seed in the autumn, large numbers of seedlings were coming up in April, 1942.

During June and July of 1941, moisture percentages of the upper three inches of soil were taken at approximately two-week intervals, samples being taken from two places on each soil type. Percentages of moisture based on oven-dry weights are given in table III.

The actual amounts of water in the soil at any one time, or the general averages, are scarcely important. When correlated with wilting coefficient (table I), however, an important difference in relative moisture availability between the two soils becomes evident. The eroded soil had an average moisture content the same as the wilting coefficient, at a depth of three inches. It was thus below the point at which water becomes non-available to the plant somewhat over half the time. The uneroded soil, on the other hand, had a water content below its wilting coefficient only once, and the general average is well above this point.

TABLE III. *Soil moisture percentages, 1941*

Date of sample	Uneroded	Eroded
May 20	7.2	7.1
	10.9	6.9
May 24	10.6	8.2
	6.3	5.1
June 3	43.3	23.3
	21.1	22.1
June 5	12.1	15.3
	12.1	14.8
June 16	6.3	5.7
	9.0	9.1
June 30	11.1	11.3
	9.2	9.5
July 14	14.3	12.7
	15.0	8.9
July 29	5.1	4.3
	1.4	5.3
Average	12.2	10.6

Results of greenhouse cultures

In the greenhouse-grown cultures of *Lespedeza stipulacea* differences in the amount of growth appeared within a few weeks after the plants were up. Except for magnitude, there was little change in the nature of these differences. Plants on the uneroded soil given treatments of calcium to saturation, calcium plus phosphorus, and phosphorus alone were dark green and apparently completely healthy. All the others showed more or less reddening of stems and russeting of leaves, and toward the end of the experiment tended to lose leaves.

Yields of *L. stipulacea* grown in the pot cultures are given in table IV. Figures given for weights and mineral content are totals of the four replications of each treatment, and the percentage composition figures are averages of the four replications. Composition figures are based on analysis of the tops. Upon examining the data a number of

TABLE IV. *Dry weights of roots and tops, and mineral analyses of tops of treated cultures of lespedeza.*

	Soil	Treatment of soil				
		Control	Ca sat.	Phos. 0.1 M.E./100 g.	K doubled Ca to sat.	Ca sat. Phos. 0.1 M.E.
Dry weight of tops	uneroded eroded	29.59 g. 16.23 g.	28.30 8.34	30.83 9.18	35.46 7.84	65.02 12.85
Total Ca	uneroded eroded	.299 g. .087 g.	.291 .058	.345 .058	.259 .052	.527 .094
Per cent Ca	uneroded eroded	1.07% .57%	1.06 .72	1.21 .68	.76 .72	.83 .77
Total Mg	uneroded eroded	.065 g. .058 g.	.059 .019	.067 .039	.06 .02	.123 .029
Per cent Mg	uneroded eroded	.22% .36%	.21 .23	.22 .43	.17 .26	.19 .23
Total K	uneroded eroded	.257 g. .139 g.	.266 .087	.302 .10	.351 .077	.604 .107
Per cent K	uneroded eroded	.87% .86%	.91 .94	.98 1.09	.99 .99	.93 .84
Total P	uneroded eroded	.843 g. 1.36 g.	.31 .10	1.84 .74	.95 .164	.65 .283
Per cent P	uneroded eroded	.285% .845%	.115 .12	.6 .813	.275 .215	.105 .22
Total N	uneroded eroded	.412 g. .178 g.	.425 .112	.53 .11	.631 .108	1.157 .176
Per cent N	uneroded eroded	1.41% 1.1%	1.60 1.35	1.72 1.2	1.77 1.39	1.78 1.37
Dry weight of roots	uneroded eroded	17.51 g. 15.34 g.	23.92 8.15	22.03 7.20	25.25 7.77	41.43 13.87

facts become evident. (1) Higher yields were obtained in all cases from the uneroded soil. (2) All treatments caused increases in yield on the uneroded soil. (3) All treatments caused at least slight decreases in yield on the eroded soil. (4) Percentage concentration of calcium in the plant tops was in all cases greater on the uneroded than on the eroded soil. (5) There was more magnesium absorption from the eroded soil, where the supply is about double that of the uneroded. (6) Percentage concentration of potassium in the plant tops remained fairly constant throughout both soils and all treatments. (7) Phosphorus was extremely variable and showed no constant relationships. (8) Percentage of nitrogen was constantly higher in the plants of the uneroded than of the eroded soil and tended to rise as the amount of growth increased. (9) Where increase in growth occurred in response to addition of nutrient to the soil, top growth tended to increase faster than root growth.

Nodulation occurred on all treatments in both soils, as in the unfertilized field plots. The root systems extended thoroughly through all parts of the soil, both the treated upper layer and the untreated subsoil, though the number of branch roots was somewhat smaller in the subsoil of the pots with eroded soil than in the uneroded and there was less penetration of the soil aggregates.

The second set of cultures, grown in 1942, confirmed for the most part the results of the first set. The data given in table V indicate that the general trend is the same. Since growth of the individual plants is regulated in large measure by competition, it is impossible to compare anything except the general trend of the differences. The nitrogen series in the second set indicate that soil nitrogen is important in growth even though some may be absorbed from nitrogen-fixing bacteria.

TABLE V. *Dry weights of tops in grams.*

Treatment	Uneroded		Eroded	
	1st set*	2nd set†	1st set	2nd set
Control	29.59	9.6	16.23	2.4
½ Ca sat.		7.0		3.2
Ca sat.	28.30	6.2	8.34	4.5
½ Ca sat. & P		11.0		6.5
Ca sat. & P	65.02	17.7	12.85	6.3
P	30.83		9.18	
Ca & K	35.46		7.84	
Ca & P & K & N		25.1		31.2
N		6.5		11.4

* Total weight of 120 plants grown in 4 replications of 30 per 3-gallon jar.

† Total weight of 15 plants grown in 5 replications of 3 per 6-inch pot.

DISCUSSION

At the beginning of the investigation it was thought that not only would yield increase in direct proportion to the nutrient added, but also the additions of nutrients would appear as increased total amount and percentage concentration of mineral in the plants grown. Neither of these original hypotheses was borne out. Yields increased on the uneroded soil, but not as greatly as was to be expected, judging from results of the Missouri Experiment Station sand-clay cultures of soybeans. (*cf.* Albrecht, '33; Horner, '36; Hutchings, '36; Graham, '38; Ferguson and Albrecht, '41.) On the eroded soils an unexpected decrease was obtained in some cases.

Careful study of the Union silt loam A and B horizons, which are the two soils represented by the "uneroded" and "eroded" soils of this experiment, shows that comparisons on an equal basis are quite impossible. Two distinct soil types, by reason of texture, structure, exchange capacity, and fertility, are actually involved. The much higher clay content of the eroded soil results not only in a much different texture and structure but also in a higher moisture retentivity and in greater exchange capacity for cations.

In these soil differences may lie the explanation for both the experimental results obtained and the hypotheses not confirmed in this study, as well as correlations with results obtained by others working along the same line. (*cf.* Hyland, '38; Stitt, '39.) The unexpected lower yield upon treatment of eroded soil with a single nutrient may possibly be explained as due to the creation of an unbalanced condition of available mineral nutrients in the soil. Since the exchange capacity is high and the nutrient supply low in the eroded soil, the addition of calcium to saturation required more calcium and produced greater disparity between calcium and other nutrients than occurred in the uneroded soil where the exchange capacity is also low and much less calcium is required to bring it to complete saturation. Loehwing ('28) has shown that in acid, muck soils this sort of injury may take place.

The second set of cultures, grown in 1942, including the addition of nitrogen alone and in conjunction with other nutrients, indicated that lack of nitrogen is certainly a limiting factor, particularly in the eroded soil. Where calcium, potassium, phosphorus, and nitrogen were added to the same culture a great improvement in growth and appearance occurred. This improvement was greatest on the eroded soil, a result which would be expected since the exchange capacity is higher and more available nutrients can be held. When these approach optimum balance with respect to relative amounts present, growth of plants improves greatly. Because of the lesser growth under conditions of complete calcium saturation in the 1941 experiments, it was thought possible that extremely high calcium might be toxic in some degree to lespedeza. However, this is apparently not the case since in the 1942 experiments, cultures with one-half calcium saturation produced less growth than the control in the uneroded soil and only slightly more in the eroded soil.

Field data taken during the course of this study indicate very definitely that physical aspects of the soil may enter into the total situation affecting the growth of plants. Wilting point determinations compared with actual moisture content of the upper three inches of soil at intervals during the summer indicate that the moisture content of the eroded soil often fell below the point of availability to plants, while on the uneroded soil it did so only infrequently. It has been shown (Pieper, Sears, and Bauer, '35) that growth of *Lespedeza stipulacea* is greatly reduced by shortage of water. This moisture difference may account for at least part of the difference in the amount of growth on the two soils, though additional soil moisture samples obtained from six and 12 inches in depth would have provided a more accurate basis of comparison with actual plant moisture relationships.

It is also probable that the amount of water held above pF 4.2 and therefore unavailable to plants (*cf.* Schofield, '35; Woodruff, '40) is so great in the eroded soil as to reduce materially the available room for air, water, and roots, thus effectively reducing the absorbing power of the plants for both water and mineral nutrients. Evidence for this suggestion is found in the fact that the eroded soil tended to remain aggregated into small lumps which were not penetrated by roots, while very little structure of any sort was evident in the uneroded soil and roots penetrated it very thoroughly. This lack of structure correlates well with the low mineral cation content of the exchange complex and the small amount of organic matter. Lack of organic matter not only reduces the supply of nutrients available to the plant, but also favors the absence of good structure and lowers the amount of water the soil is able to hold.

The data obtained as to percentage composition of the plants grown on the uneroded soil follow in most instances the results obtained by others doing experiments of the same general type (*cf.* Vanderford, '41; Weathers, '38). Results on the eroded soil show little correlation. Differences in yield on either soil correlate with percentage concentration differences in some cases and in others they do not.

In every instance the percentage of calcium in the plant tops was greater in plants grown on the uneroded than on the eroded soil. This was expected in the controls, since the uneroded soil is 55 per cent saturated with calcium as compared with 36 per cent in the eroded soil and plants are thus able to absorb calcium more efficiently. It apparently also holds true in the treated samples. Where growth did not increase, concentration of calcium did not increase, even though the total calcium in the plants on the uneroded soil was much higher than in those on the eroded soil. Addition of calcium and phosphorus together produced better growth, with the result that more calcium at a lower concentration was absorbed by the plants. Apparently more efficient use is made of it by the plant.

Percentage concentration of potassium remained fairly constant with some indication of increase where the supply was increased in relation to calcium and where the efficiency of the plant was increased through added phosphorus. This is in agreement with the results of others working on calcium and potassium nutrition. It appears unlikely that potassium was seriously deficient in these soils. Absorption of magnesium followed the pattern expected from the results of Graham ('38) who found that in sand-clay cultures of soybeans absorption varied according to the amount present. Greater absorption was consistently obtained from the eroded soil, where the amount of magnesium present was double that of the uneroded.

Both total amount and percentage of nitrogen, unlike the other nutrient elements, rose as the growth of the plant increased. There was consistently a higher amount in the plants grown on uneroded than on eroded soil. This is to be expected since the activity of nitrogen-fixing bacteria is related to the extent of growth rather than to soil factors directly. As the health of the plant increases through the approach of the available nutrient supply to the optimum the amount of nitrogen fixed is increased.

When phosphorus alone was added to the soil a high percentage was absorbed by the plants but little increase in growth occurred. When both phosphorus and calcium were added, growth increased markedly but the percentage of phosphorus was much lower. Apparently calcium and phosphorus are linked in the nutrition of the plant, though in this situation it is not a case of the addition of calcium increasing the absorption of phosphorus as was found by Albrecht and Klemme ('39) and Albrecht and Smith ('39).

Allard ('42) has reported a study of plant growth on soil of barren patches similar in many respects to the eroded soil herein discussed. After comparing results of various nutrient treatments, he concluded that the limiting factor in growth was lack of available phosphorus and nitrogen. The data presented in this paper compare very favorably with Allard's results wherever similar treatments were given. In Allard's work, phosphorus was added to greenhouse cultures only in conjunction with other nutrients while in the field it was added with only nitrogen and potassium. Since growth on his field plots was poor, he concluded that the soil probably had a high fixation capacity for phosphorus. In the light of the data from this investigation, which indicate that phosphorus alone produces little increase in growth, it seems likely that this effect in Allard's results may rather have been caused by a lack of nutrient balance in the field treatments. Thorough soil tests before and after addition of phosphorus and also comparisons with normal soils in the same area would have helped considerably to clarify this point. Moreover, physical characteristics of the soil, though not considered by Allard, should probably have been taken into consideration.

The ratio of yields of *Lespedeza stipulacea* in the field paralleled very closely that obtained from the control cultures in the greenhouse. About twice as much growth was produced on the uneroded as on the eroded soil. Since this is true and since addition of mineral nutrients caused no increase in growth on the eroded soil, it appears possible that physical factors related to structure may be more important than chemical factors in the diminution of growth on the eroded soil. Physical factors also appear to be important in the severe frost-heaving and winter-killing of *Lespedeza sericea* on the eroded site.

Competition of weeds was not a factor of paramount importance in establishment, but on the eroded soil, at least, where weed growth was good it operated to reduce the yield of all three species of lespedeza. Numbers of individuals were definitely reduced, though only slightly in the case of plots of *L. virginica* on eroded soil. Furthermore, there is an indication that the perennials on the unweeded areas survived the winter somewhat better than where there had been no competition. At the beginning of the second year, however, no difference was observable between either weeded and unweeded or eroded and uneroded sites in respect to the number of seedlings of *L. stipulacea* which appeared. Large numbers came up on all areas. Cassia failed to become re-established adequately the second year, when only scattered seedlings came up, possibly because the seed was eaten by birds or mammals during the winter.

Lespedeza sericea survived up to about 70 per cent on the uneroded soil but less than 5 per cent on the eroded soil. About 90–96 per cent of the *L. virginica* survived on both soils. Thus *L. sericea* does not appear to be suited to planting on this sort of severely eroded area while *L. virginica* has definite possibilities. Both *L. stipulacea* and *Cassia fasciculata* grow well but *Cassia* is not adequately re-established while *L. stipulacea* is. A combination of *L. virginica* with one of the annuals might well have possibilities for cover planting of eroded soils of this type. These preliminary investigations indicate that soil treatments should be designed to produce better soil structure as well as to add a balanced supply of nutrients, but no specific treatments have yet been found which yield practical results on such severely eroded areas.

Summary and Conclusions

An investigation was conducted regarding the establishment and growth of three species of lespedeza, *L. stipulacea*, *L. sericea*, and *L. virginica*, and *Cassia fasciculata* on eroded and uneroded areas of Union silt loam under conditions of competition and absence of competition. By means of additions of mineral nutrients to pot cultures of *L. stipulacea* under greenhouse conditions determination of the specific soil factors involved was attempted.

Analyses were made of both soils; quadrat counts were made and weights measured of plants on the field plots; and weight records and mineral analyses of plants grown in the greenhouse were made. On the basis of these results certain general conclusions may be drawn.

1. Two distinct soil types are to be dealt with in comparing these eroded and uneroded soils.
2. Yields are from 50 to 100 per cent higher on the uneroded soil.
3. Growth of *Lespedeza stipulacea* is reduced by competition and is less on eroded soil, but adequate re-establishment takes place the second year on all areas.
4. *Cassia fasciculata* does well on both areas but is not adequately re-established the second year.
5. *Lespedeza sericea* and *L. virginica* become established equally well on both soils the first year, but *L. sericea* does not well survive the winter on the eroded soil while *L. virginica* does. Competition affects growth the first year, but does not have much effect on survival or growth the second one.
6. The same pot treatments—meeting of lime requirement, added potassium, and added phosphorus—give completely differing results. They are effective on the uneroded and completely ineffective on the eroded soil. No single treatment, except possibly the addition of nitrogen, will aid plant growth on the eroded soil and may even be harmful. However, several nutrients added together, including nitrogen, produce definitely increased growth on the eroded site.
7. Water availability, and soil texture and structure may be important as factors in growth on these particular soils.
8. Concentration of minerals in the plant vary with the soil rather than with the treatment applied.

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FACTORS INFLUENCING THE UPSTREAM MIGRATION OF THE PINK SALMON (*ONCORHYNCHUS GORBUSCHA*)

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Introduction

The pink salmon are found in the waters along the Pacific Coast from the Columbia River to the Bering Sea but are most abundant in southeastern Alaska, where they spawn by the millions each year.[1] This part of Alaska is composed of a narrow strip of continental land that is bordered by a large and broken chain of mountainous islands which protect it from the sea. Owing to the temperate climate and heavy rainfall in the region (see fig. 1) most of the islands and mainland shore are covered with dense growths of timber (spruce, hemlock and cedar) and are drained by hundreds of streams that range in size from brooks to small rivers. These streams may be separated into two groups: first, those originating in lakes, and second, those originating in mountain slopes or watersheds with little or no storage capacity. The former have a more or less steady flow, for the lakes act as reservoirs for the melting snow and rainfall, whereas the latter being fed mainly by surface run-off, have an

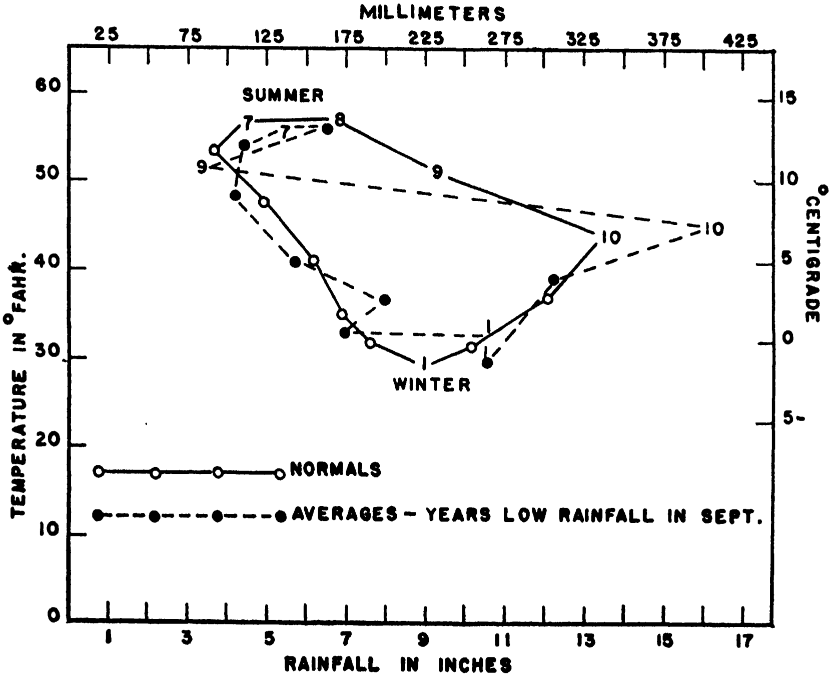

Fig. 1. The hythergraph (temperature-rainfall) for southeast Alaska. The normal mean monthly temperature is plotted to the normal total monthly rainfall for each month of the year. The numbers inserted in the graphs indicate the months of the year. The graph giving the temperature and rainfall in years of low rainfall in September consists of the average of 5 years during each of which this condition occurred. The data represent the average of observations taken at 6 stations located at various points in southeast Alaska.

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[1] For a detailed description of the life history of the pink salmon, see Davidson ('34) and Pritchard ('39).

exceedingly variable flow which is dependent, for the most part, upon the immediate precipitation in their watersheds.

The majority of the streams in southeastern Alaska fall within this latter group and in years with abnormally low rainfall in September, serious mortality occurs in the pink salmon populations spawning in them. From the temperature-rainfall graphs in figure 1, it will be noted that the rainfall in southeastern Alaska is normally lowest in June and highest in October, increasing each month from June to October. Since the pink salmon as a rule do not begin their spawning migration until the first week in July there is sufficient water in the streams in years of normal rainfall to carry them through to September at which time spawning is well under way. There are, however, occasional years when the rainfall is lowest in September and during these years the pink salmon spawning in this latter group of streams become biologically trapped in them and die by the thousands. The strong positive reaction of the salmon to current, together with their inherent urge to remain on the spawning beds when sexually mature, inhibits a general downstream migration to the bays with the receding flow as the rainfall decreases. Most of the salmon remain in the shallow pools until they become exposed and perish.

From surveys of the important pink salmon producing streams in southeastern Alaska it was found that the character of the upstream migration of this species is not the same in all of them and that it appears to depend more upon the inherent behavior of the fish than upon the environmental conditions in the streams. From the standpoint of behavior there are roughly two types of upstream migration and neither one appears to be limited to streams with specific environmental conditions.

The first type may be described as follows: the salmon as they arrive in the bays during the course of the inshore migration or run congregate off the mouths of the streams where they remain until sexually mature and ready to spawn before continuing their migration into them.[2] This behavior of the salmon takes place even though the flow in the streams may be favorable to their upstream movement. However, upon reaching sexual maturity, they will attempt to enter the streams regardless of the water level. Populations of salmon following this type of upstream migration linger in the bays from 15 to 35 days before entering the streams.

The second type of upstream migration differs considerably from the first type. The salmon as they arrive at the mouths of the streams during the course of the run, will, after a few days of apparent adjustment to fresh water, attempt to migrate into them. If the flow in the streams is favorable to their upstream movement, the salmon will enter them readily and continue upstream to collect in the deep pools where they remain until ready to spawn. If, however, the flow of the streams is such that it is difficult for the salmon to enter them, they will remain in the bays until the flow becomes favorable to their entrance. Upstream migrations of this type are closely related to the flow in the streams which in turn depends upon the character of their watersheds and the amount of precipitation during the migratory season. Salmon following this type of upstream migration, if forced by unfavorable stream conditions to remain in the bays until they become sexually mature, will upon the attainment of sexual maturity also attempt to enter the streams regardless of the flow.

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[2] The first salmon to appear in the run, although of adult size, are sexually immature. As the run progresses in the season, however, sexual development becomes more and more pronounced in the fish composing it, until those appearing in the last of the run are fully mature and within a few days of spawning. The rate at which sexual development takes place in the pink salmon and the physical and chemical changes involved are described by Davidson ('35) and Davidson and Shostrom ('36).

Observations have been made during the past decade on the daily variations in stream level, certain physico-chemical properties of the water, and the upstream movement of the pink salmon in three streams. This study is based upon the analysis of the data collected through these observations and presents a quantitative interpretation of the influence of the various environmental factors on the upstream migration of the salmon.

SOURCE OF DATA

The data which form the basis of this study were collected from three streams, namely, Sashin Creek and Snake Creek in southeastern Alaska and McClinton Creek in British Columbia.

Sashin Creek is the only stream flowing into Little Port Walter on Baranof Island. It has a large mountain lake of the same name in its watershed. A weir or picket fence, through which the adult salmon are counted as they migrate upstream, has been operated in this stream each season since 1934. From 1934 to 1938, inclusive, daily records were kept of the stream temperature by means of a recording thermograph and of stream level through two readings a day, morning and evening. Daily precipitation and air temperatures have been recorded at this location, according to the United States Weather Bureau methods, since 1936.

Snake Creek is the main stream flowing into Olive Cove on Etolin Island. It originates in a number of mountain lakes. A counting weir was operated in this stream each season from 1930 to 1933, inclusive. During these seasons daily records were kept of the stream temperature by means of a recording thermograph and of stream level through two readings a day, morning and evening. In the 1930, 1931 and 1932 seasons, hydrogen-ion determinations were made of the water in the stream and bay at regular intervals.

McClinton Creek is the main stream flowing into McClinton Bay on Graham Island, which is in British Columbia just south of the border that separates British Columbia and southeastern Alaska. It originates in mountain slopes and has very little storage capacity in its watershed. An upstream counting weir was operated in this stream in 1932 and 1934.[3] Daily records were also kept of the stream temperature, water height and rainfall during the migratory period of the salmon. Stream temperatures were recorded from two daily readings, morning and evening. Water height was recorded daily both in the morning and evening. Rainfall was collected daily in a standard gauge supplied by the Dominion of Canada Meteorological Service.

UPSTREAM MIGRATION IN SASHIN CREEK

Sashin Creek, at Little Port Walter, originates in three mountain lakes, whose total area is approximately 1½ square miles, and maintains a flow sufficient for the salmon to enter it at all times during the inshore migratory season. A heavy shower will produce a rather rapid rise in the stream but owing to the lake storage in its watershed, it gradually recedes and does not drop abruptly within a day or two after the shower. The salmon spawn only in the lower part of the stream for a 60 foot falls occurs ¾ mile from its mouth that prevents their further ascent. In the area in which spawning takes place the stream averages 60 feet in width and during periods of little or no rainfall it fluctuates around 12 inches in depth.

Adult pink salmon begin to appear in the bay at Little Port Walter each year about the second week in July. This marks the beginning of the run, inshore migration, which usually continues through the first week in September. The salmon congregate in the bay as the run progresses and do not enter the stream until they are sexually mature and ready to spawn. The first salmon to arrive in the bay become sexually mature about the middle of August at which time they school up at the mouth of the stream and move into it. This marks the beginning of the upstream migration. The males that migrate into the stream have fully developed second-

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[3] Owing to the complete two year life cycle of the pink salmon the odd and even year runs are wholly independent of each other and it is not too uncommon to find streams in which only the odd or even year run persists. See Davidson ('34) and Pritchard ('39).

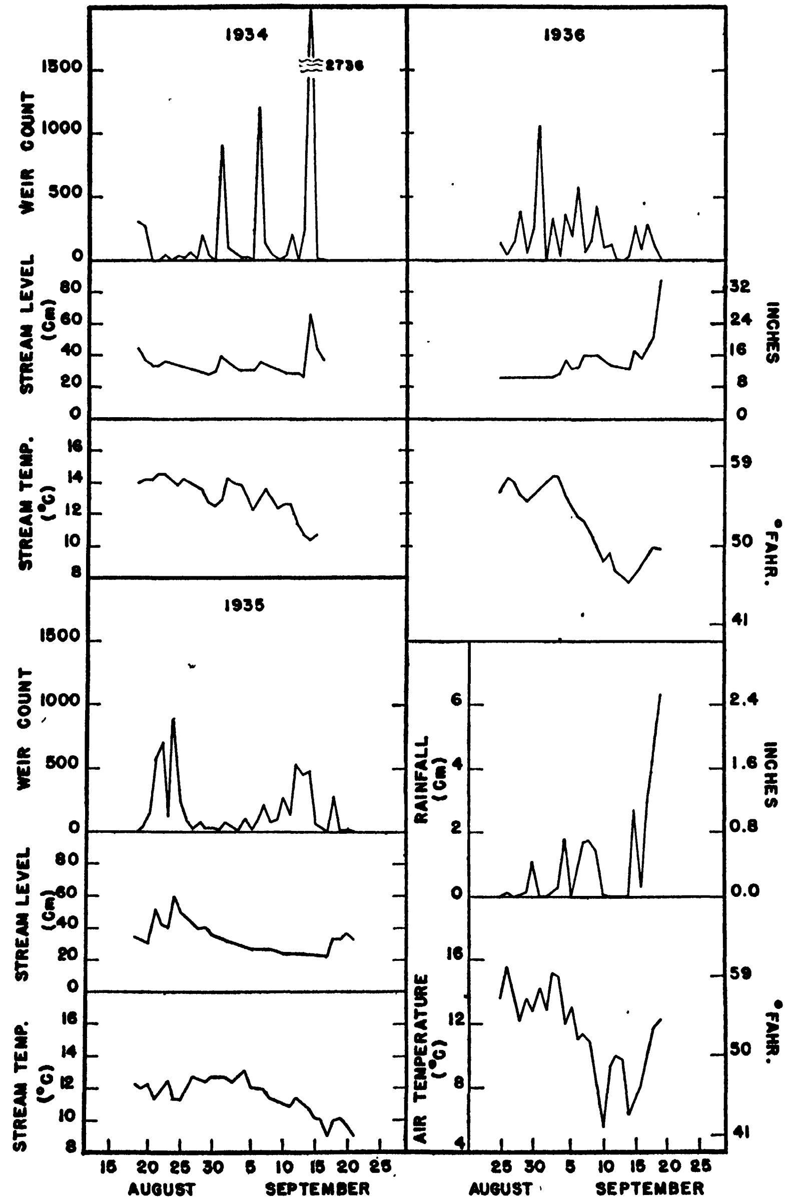

FIG. 2. Daily average stream temperature and stream level and number of pink salmon (daily weir count) migrating into Sashin Creek, Alaska, in 1934, 1935 and 1936.

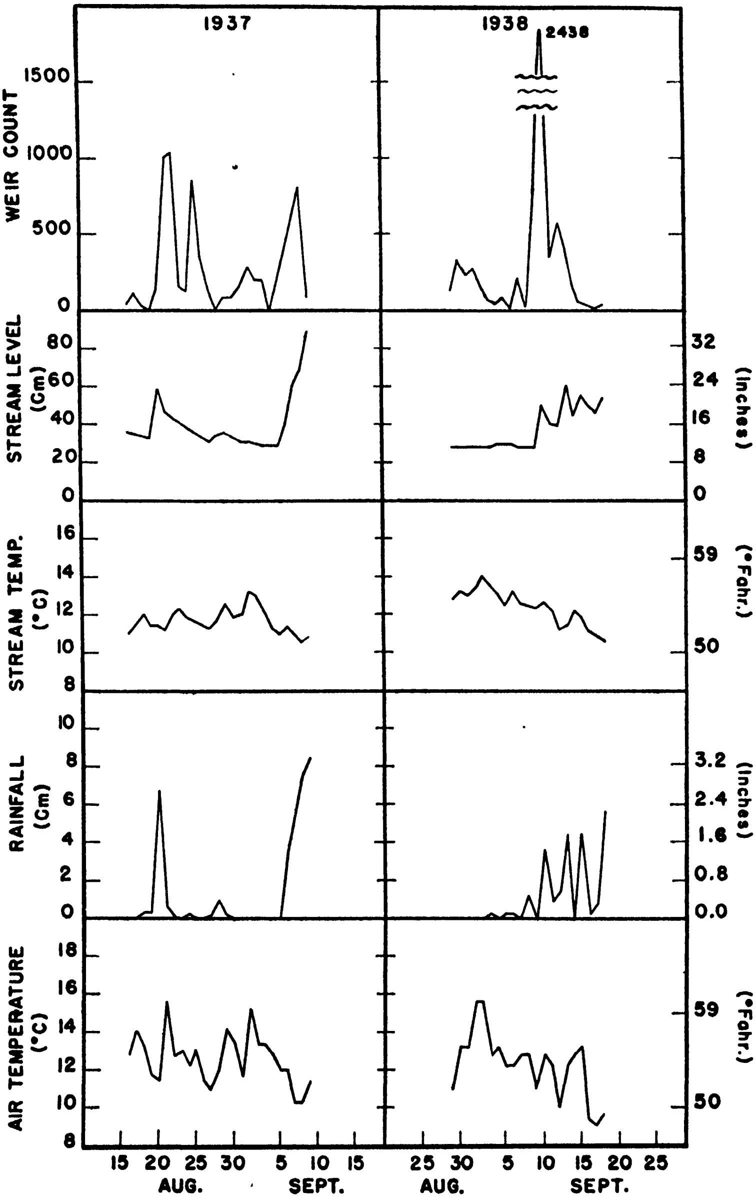

FIG. 3. Daily average air temperature, stream temperature and stream level; daily rainfall and number of pink salmon (daily weir count) migrating into Sashin Creek, Alaska, in 1937 and 1938.

ary sexual characters which consist of a greatly elongated snout and large dorsal hump. They are readily distinguished from the females whose body form changes very little with sexual development.

The attainment of sexual maturity by the salmon before starting their upstream migration is so consistent, that owing to the marked change in the body form of the sexually mature males, all of the fish may be accurately tallied as to their sex as they are counted through the weir.

The daily weir count of pink salmon into Sashin Creek and the average daily level and temperature of the stream for each season from 1934 to 1938, inclusive, are given graphically in figures 2 and 3. The daily rainfall and average daily air temperature in the watershed of Sashin Creek during the 1936, 1937 and 1938 seasons are also given in figures 2 and 3. An inspection of these graphs will show that the upstream movement of the pink salmon in Sashin Creek as measured by the daily weir count was just as active during periods of low stream level as during periods of high stream level. For example, in the 1936 season the highest daily weir count occurred during the period when the stream was at mean low level, and it was also during this period that 46 per cent of the total run moved into the stream. In the 1935, 1937 and 1938 seasons, large daily weir counts occurred during periods of both high and low water. In the 1938 season the salmon began to move into the stream when the water was at mean low level. On September 9, when the stream was at its lowest level the weir count rose to the second highest point in the season. On September 10th, it rained, the stream level increased and the weir count reached its highest point in the season. Although the water level increased following September 10th the weir count gradually decreased, for 76 per cent of the run had already entered the stream. In fact, 52 per cent of the run moved into the stream on September 9th and 10th.

In a comparison of the daily weir counts to the average daily stream temperature, as given in figures 2 and 3, it will be seen that the upstream movement of the salmon was likewise just as active during periods of relatively high stream temperature as during periods of low stream temperature. In other words it appears that upon the attainment of sexual maturity, the salmon schooled up at the mouth of the stream and moved into it regardless of the level of the water or its temperature.

In the study of the migration of a number of species of wild animals it has been found that sudden changes in temperature and other environmental factors play an important role in stimulating their migratory movements. In view of the stimulating influence sudden changes in stream level and stream temperature may have had upon the upstream movement of the salmon, once they had collected at the mouth of the stream, correlations were computed between the daily deviations in weir count and the daily deviations in stream level and temperature from their respective seasonal trends. The coefficients of these correlations are given in table I.

TABLE I. *Correlation coefficients between daily variations in stream level, stream temperature and the upstream movement of the salmon (weir count) in Snake Creek, 1930 to 1933, and Sashin Creek, 1934 to 1938.*

Location and Year	Coefficients of Correlation between			
	Weir Count and Stream Level		Weir Count and Stream Temperature	
	$r \pm \sigma_r$	P_r	$r \pm \sigma_r$	P_r
Snake Creek:				
1930	−0.222 ±0.163	>0.10	0.038 ±0.171	>0.10
1931	0.556 ±0.101	<0.01	−0.254 ±0.136	0.07
1932	−0.311 ±0.138	0.04	−0.046 ±0.152	>0.10
1933	−0.235 ±0.151	>0.10	0.190 ±0.154	>0.10
Sashin Creek:				
1934	0.766 ±0.080	<0.01	−0.199 ±0.185	>0.10
1935	0.749 ±0.076	<0.01	−0.080 ±0.173	>0.10
1936	0.023 ±0.204	>0.10	−0.019 ±0.204	>0.10
1937	−0.021 ±0.208	>0.10	−0.034 ±0.208	>0.10
1938	0.522 ±0.209	0.01	0.081 ±0.222	>0.10

r: Pearson's coefficient of correlation.
σ_r: Standard error of the coefficient of correlation.
P_r: A coefficient of correlation whose probability value (P_r) is less than 0.05 is considered statistically significant; one whose value is greater than 0.05 is not considered statistically significant.

The coefficients of the correlations between the daily variations in weir count and stream level were rather high and statistically significant in the 1934, 1935 and 1938 seasons but were negligible in the 1936 and 1937 seasons. The significant positive correlation between these variables in 1934, 1935 and 1938 may be attributed to the coincident occurrence of abrupt daily increases of considerable magnitude in weir count and stream level. In figure 2 it will be seen that on three occasions during the 1934 season large numbers of salmon moved into the stream on the days sudden increases occurred in the stream level. Although the stream level did not drop abruptly the next day, the weir count did, thus showing that most of the salmon collected at the mouth of the stream preparatory to entering it moved upstream the first day of the increase in stream level. A similar coincidence occurrence between abrupt increases of considerable magnitude in weir count and stream level took place during the first part of the season in 1935 and on September 10th in 1938. The coincident occurrence of abrupt increases in weir count and stream level in the 1936 and 1937 seasons were not of sufficient magnitude to bring about a significant positive correlation between weir count and stream level in these years.

The coefficients of correlation between the daily variations in weir count and stream temperature were negligible in all of the years. The coefficients of correlation between the daily variations in stream level and stream temperature were also negligible thus indicating that stream temperature fluctuated independently of stream level. In fact, the daily variations as well as the seasonal trends in stream temperature were very closely associated with changes in air temperature. The coefficients of correlation between these variables in 1936, 1937 and 1938 ranged from 0.6 to 0.9 and were statistically significant in each case.

From this analysis, it appears that sudden changes in the water level of the stream or the factors closely associated with it may stimulate the upstream movement of the salmon once they have congregated at the mouth of the stream preparatory to entering it. However, unless the salmon are sexually mature and ready to enter the stream they do not react to changes in its water level. There appears to be no relationship whatsoever between the variations in stream temperature and the upstream movement of the salmon.

UPSTREAM MIGRATION IN SNAKE CREEK

Snake Creek at Olive Cove originates in a group of five mountain lakes, whose total area is approximately 2½ square miles, and like Sashin Creek, maintains a flow great enough for the salmon to enter it at all times during the inshore migratory season. It is also similar to Sashin Creek in that a heavy shower will produce a rather rapid rise in its water level but the run-off is more or less gradual. In fact, both of these streams are typical of the streams classified in group one.

The stream does not flow directly into the bay but empties into a large brackish lagoon that is connected with the bay by a narrow channel. A ten-foot falls occurs in the stream at the point where it empties into the lagoon. For the first ¼ mile above this falls the stream averages 90 feet in width and 4 feet in depth and flows quietly over a sandy-mud bottom. Above this quarter mile of quiet water, the stream averages 75 feet in width and 12 inches in depth and flows swiftly over a clean gravel bottom. A 90 foot falls occurs in the stream 1½ miles above the stretch of quiet water and marks the farthest point of ascent by the salmon.

Adult pink salmon begin to appear in the bay at Olive Cove about the second week in July. This marks the beginning of the run that usually continues to the last of August. The salmon remain in the bay for a few days and then move into the brackish lagoon where they collect in a deep pool below the 10 foot falls at the mouth of the stream. The salmon have no difficulty in ascending this falls, except during heavy freshets, and move directly into the stream where they congregate in the ¼ mile stretch of

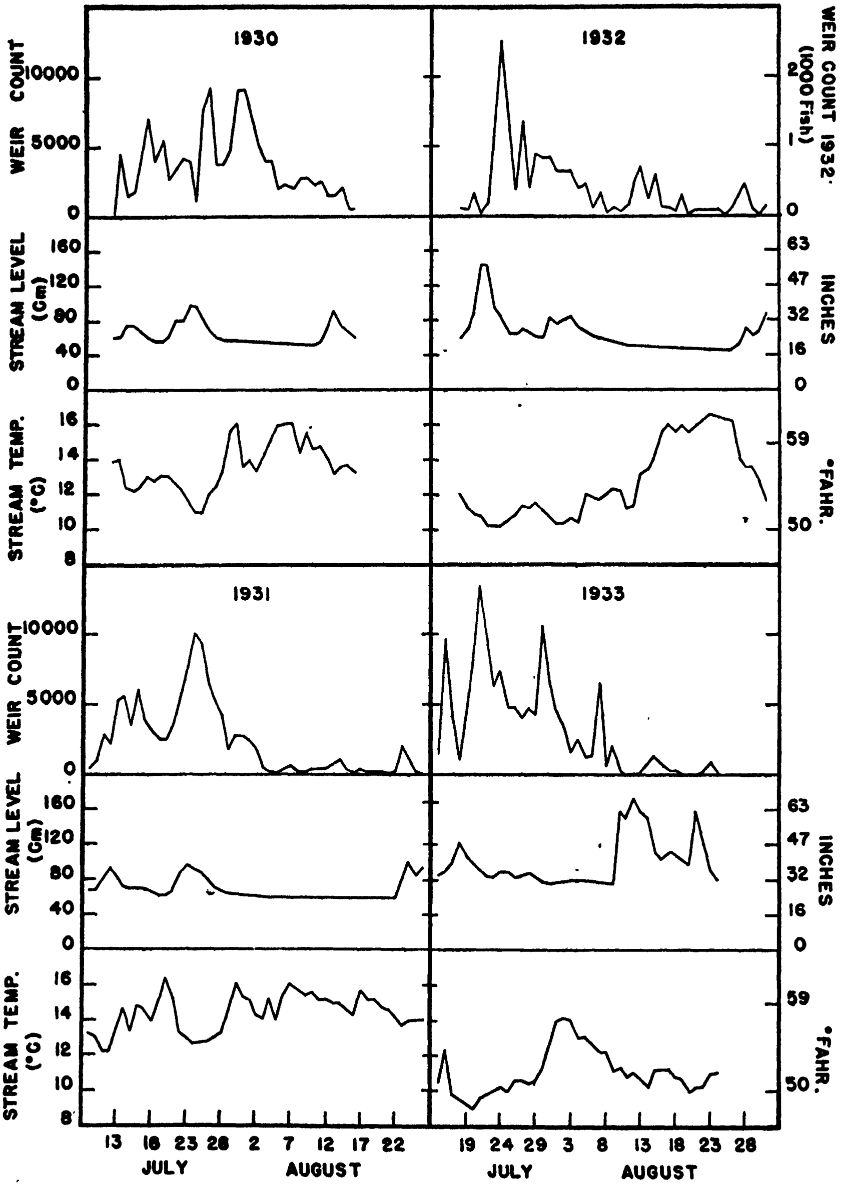

FIG. 4. Daily average stream temperature and stream level and number of pink salmon (daily weir count) migrating into Snake Creek, Alaska, in 1930 to 1933, inclusive.

comparatively quiet water. They mill slowly about in this part of the stream until they become sexually mature and ready to spawn. This usually takes place towards the end of the run, last of August, when the fish entering the stream are also sexually mature and the whole population moves upstream into the 1½ miles of swift shallow water to spawn.

The daily weir counts of pink salmon into Snake Creek and the average daily level and temperature of the stream are given graphically in figure 4. An inspection of these graphs will show that the upstream movement of the salmon was just as active during periods of relatively high stream level as during periods of low stream level. For example, in 1930 half of the run entered the stream during a period when the water level was 2 feet or greater and half came during the period the water level was under 2 feet. There was likewise very little relationship between the upstream movement of the salmon and the level of the stream temperature. In 1930, half of the run entered the stream during a period when the water temperature was 13° C. or under and the other half entered the stream when the temperature was considerably over 13° C. A similar situation occurred during the run in 1931.

Here, as in the analysis of the Sashin Creek data, correlations were computed between daily deviations of weir count and the daily deviations of stream level and temperature from their respective seasonal trends. The coefficients of these correlations are given in table I. The coefficients of the correlations between weir count and stream level in 1930, 1932 and 1933 were negative in sign and small. The negative character of these coefficients may be interpreted as being due to the slight but consistent inhibitory influence of the current associated with sudden increases in water level upon the ascent of the salmon over the falls at the mouth of the stream. In fact when the water rises much above 4 feet the current becomes so strong over the falls that very few salmon can surmount them.

In 1931 the coefficient of correlation between weir count and stream level was positive and statistically significant. This positive correlation was due mainly to the coincident occurrence of large numbers of pink salmon in the run during the brief period from July 20 to 28 when the amount of water in the stream fluctuated at a rather high level.[4] The daily number of salmon entering the stream at the beginning of the 1931 run increased at a rather rapid rate for the first five days and then began to decline in a similar manner. This decline in the daily weir count was not due to the simultaneous occurrence of unfavorable conditions at the mouth of the stream but to a marked decrease in the numbers of salmon entering the bay and lagoon. From July 10 to 19, the weather was fair and warm, and the lack of rainfall together with the increased evaporation, brought about a marked reduction in the flow of the streams in the region. During periods of dry weather, when there is little fresh water entering the bays the salmon have a tendency to tarry in the larger and more open channels and do not move inshore until rainfall increases the flow of the streams. The continued dry weather from July 10 to 19 temporarily retarded the inshore migration of the Snake Creek run and it was not until the rains started on July 20 that the salmon began to appear in the bay again in large numbers. From July 20 to 28 there was a great influx of fish into the bay. In fact 50 per cent of the entire run occurred during this brief period and the fish moved upstream as rapidly as they entered the bay. Therefore, although a very marked positive relationship occurred between weir count and stream level from July 20 to 28, it was due not to a more favorable influence of stream level on the upstream movement of the salmon but to the occurrence of unusually large numbers of fish in the run during this brief period of rainy weather in an otherwise fair and warm season.

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[4] The salmon composing the 1931 run were somewhat larger than those in the 1930, '32 and '33 runs (Davidson and Vaughan '41) and were therefore better equipped to surmount the falls during periods of increased flow. Pritchard ('36) observed that the coho and chum salmon which are considerably larger than the pink salmon were able to swim upstream against a much stronger current. In other words, the size of the fish makes a considerable difference in its ability to swim against the current and surmount difficult falls.

The coefficients of correlation between the daily deviations in weir count and the daily deviations in stream temperature (see table I) were small, inconsistent in sign and of no statistical significance. Here, as in Sashin Creek, the daily variations as well as the seasonal trends in stream temperature were closely associated with changes in air temperature. The coefficients of correlation between these variables ranged from 0.45 to 0.73 and were statistically significant in each case.

In the summer of 1930, the hydrogen-ion concentration of the water in the stream and in the bay was taken at daily intervals. The pH values in the stream fluctuated between 6.1 and 6.3 and there was no indication of any relationship between the upstream movement of the salmon and the fluctuations in these values. The pH values of the water in the bay ranged between 8.2 and 8.4 depending upon the stage of the tide and their fluctuations also bore no relationship to the daily movement of the salmon into the stream. Hydrogen-ion concentration readings in the stream and bay were taken during the summers of 1931 and 1932 for checking the 1930 data. In both of these summers the pH values fluctuated in a manner similar to that in 1930.

The high falls in the stream at the upper end of the area in which the salmon spawn and the falls at the mouth of the stream completely aerate the water and keep its oxygen content near the maximum. The buffer content of the water in the stream is almost negligible, being 2 to 6 parts per million methyl red alkalinity. In fact the water is about as pure chemically as any that can be found under natural conditions.

From this analysis, it appears that the daily movement of the pink salmon into Snake Creek follows the course of the inshore migration, approximating a rising and then falling trend, and is not related in any significant degree with fluctuations in the known physical and chemical conditions in the stream.

UPSTREAM MIGRATION IN McCLINTON CREEK

McClinton Creek at McClinton Bay originates in mountain slopes and has very little storage capacity in its watershed. It depends entirely upon surface run-off and underground seepage and during the inshore migration of the salmon its flow is closely related to the daily rainfall in its watershed. A heavy shower will produce a rapid increase in the flow of the stream and, owing to the lack of storage in the watershed, it usually recedes in a similar manner after the shower. The width of the stream varies from 60 feet near the mouth to 20 feet, 2½ miles above the mouth. The depth changes with the weather and varies from 6 inches during dry spells to over 6 feet at the peak of heavy freshets. A number of holes from 8 feet to 15 feet deep occur in the first 4,200 yards above the weir. This is the area in which the salmon spawn but the upper end starting at about 3,000 yards is rocky and supports only a limited number of fish.

Adult pink salmon begin to appear at the head of the bay off the mouth of McClinton Creek late in the month of August of each even-numbered year. The fish arriving in the bay at this time are sexually immature and the males show very little indication of the development of their secondary sexual characters. If the water level in the stream is up and showers occur from day to day, the salmon will move directly into the stream and congregate in the deep holes in the area where spawning takes place. If, on the other hand, the water level in the stream is low and dry weather continues the salmon will mill about in the bay until it rains and the stream flow increases. During periods of dry weather only an occasional salmon enters the stream at high tide or on the first of the ebb. However, if the salmon become sexually mature and ready to spawn before rainfall occurs they will attempt to move into the stream regardless of its water level. Hence the run of pink salmon at McClinton Creek normally follows a type two upstream migration but may turn into a type one migration under certain environmental conditions.

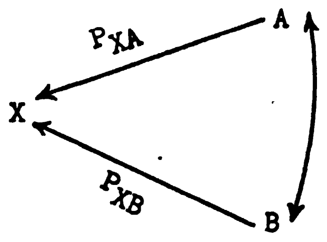
Pritchard ('36) described the upstream migration of the pink salmon in McClinton Creek in 1932 and 1934 and studied the influence of rainfall on stream height and the influence of both these factors upon the upstream movement of the salmon. Coefficients of correlation were calculated between these variables and with one exception they were quite high and statistically significant, thus showing that a substantial relationship (covariation) existed between them.

In order to derive a quantitative interpretation of the influence of rainfall on stream height and stream height on the upstream movement of the salmon a more complete correlation analysis was made of the data.

CORRELATION AND CAUSATION

The coefficient of correlation may well be called the coefficient of covariation for it essentially is a measure of the degree of association between the variations in two sets of values. Its presence does not necessarily imply a relationship of cause and effect between the variations in the two sets of values. However, where such a relationship exists, the set of values whose variation is affected is known as the dependent variable or effect and the set of values whose variation produces the effect is known as the independent variable or cause. Under certain conditions the variation in the dependent variable may be due entirely to the variation in the independent variable. For example, if the variation in X, the dependent variable, be due entirely to the variation in A, the independent variable, then the coefficient of correlation between X and A, r_{XA}, would be ± 1.0, or perfect correlation. Such cases of complete causal relationship between the dependent and independent variable are rare in occurrence. In most cases the variation in the dependent variable is produced by the variations in two or more independent variables. For example, if the variation in X is completely produced by the variations in A and B, which are independent variables, but unrelated to each other, r_{XA} could equal 0.8 and r_{XB} equal 0.6. In this case, each of the independent variables is responsible for a certain percentage of the total variation in X. Since the square of the coefficient of correlation measures the portion (percentage) of variability in the dependent variable which is produced by the independent variable, A in the above example produces 64 per cent of the variation in X and B produces 36 per cent, or together both produce 100 per cent, or the total variation in X. If however, A and B are related, i.e., a correlation exists between them, then a different method must be used in calculating the degree of determination of X by A and B.

Wright ('34) in studying systems of correlated variables developed the method of path coefficients for calculating the degree of direct influence of each independent variable or cause in a series of interrelated causes. A system of variables in which X is completely determined by the interrelated variables A and B may be illustrated by the following diagram, with the mathematical relationships between X, A and B represented by the constants:



$r_{XA} = 0.9490$

$r_{XB} = 0.5547$

$r_{AB} = 0.2640$

$p_{XA} = 0.8627$

$p_{XB} = 0.3269$

$d_{XA} = 0.7442$

$d_{XB} = 0.1069$

$d_{X\overline{AB}} = 0.1489$

By definition (Wright, '34), the path coefficient for the path from A to X, p_{XA}, measures the direct influence of A on X and is the ratio of the standard deviation in X due to A to the total standard deviation in X. The coefficient of determination of X by A, d_{XA}, is the square of p_{XA} and measures the fraction of the total variation in X for which A is directly responsible. The relation of the path coefficient to the coefficient of correlation is given in the equations:

$$r_{XA} = p_{XA} + p_{XB}r_{AB}$$
$$r_{XB} = p_{XB} + p_{XA}r_{AB}$$

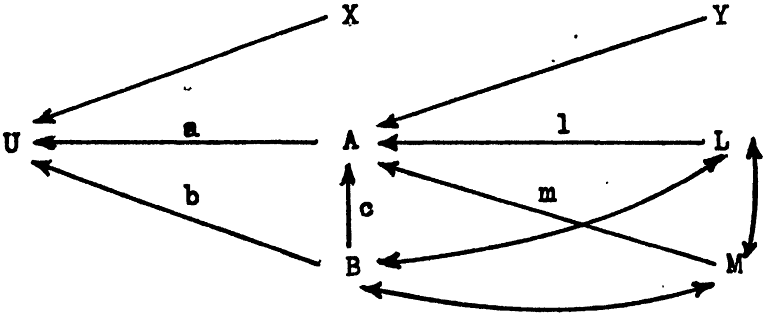
In these equations p_{XA} represents the direct influence of A on X and $p_{XB}r_{AB}$ represents its indirect influence on X. The values of p_{XA} and p_{XB} are essential in determining that portion of the variability in X that is due to A and B independently and that which is due to A and B combined. In this example, d_{XA} equals 0.7442 and d_{XB} equals 0.1069. Therefore A is directly responsible for 74.42 per cent and B is directly responsible for 10.69 per cent of the total variability in X. Since the sum of these two constants is only 85.11 per cent there still remains a portion of the total variability in X that is due to the combined or mutual influence of A and B on X. The value of this portion is determined by the equation:

$$d_{X\overline{AB}} = 2p_{XA}p_{XB}r_{AB} = 0.1489$$

This method may be readily expanded in the analysis of complex systems of variables and is not only exceedingly valuable in determining the amount of variation in a dependent variable that is due to the influence of known causal factors but also in determining the amount of residual variation in the variables that is due to the influence of unknown factors or those for which quantitative data are not available. This type of analysis provides a means of combining the information given by the coefficients of correlation between interrelated variables with such information as may be at hand with regard to the interdependence of these variables and thus makes quantitative an interpretation of the causal relationships involved which would otherwise be merely qualitative.

Analysis of McClinton Creek Data

The interrelationship of rainfall and water height and their possible paths of influence upon the upstream movement of the salmon in McClinton Creek may be described graphically in the following diagram:



where, U is the number of pink salmon migrating into the stream each day as determined by the daily weir count; A is the maximum stream height; L is the total rainfall on the same day as the weir count; B is the maximum stream height the day before, or 24 hours previously; M is the total rainfall 24 hours previously; X represents the other causes or factors not associated with stream level that influence the rate of movement of the salmon into the stream;

and Y represents factors that affect stream level other than immediate rainfall, such as springs and seepage from underground drainage. Although these latter factors are the result of annual precipitation in the watershed of the stream they are not influenced to an appreciable extent by the immediate rainfall. a, b, c, l and m are the coefficients of the paths of influence of the various factors upon each other as illustrated in the diagram. The single arrows indicate the direction of the reactions along the paths of influence and the double arrows indicate correlations between the factors.

The path coefficients $p_{UA} = a$, $p_{UB} = b$, $p_{AL} = l$, $p_{AM} = m$ and $p_{AB} = c$ were calculated from the following equations by substituting the values of the coefficients of correlation in them and solving for the path coefficients.

$$
\begin{aligned}
r_{UA} &= a + br_{AB} \\
r_{UB} &= ar_{AB} + b \\
r_{AL} &= l + mr_{LM} + cr_{LB} \\
r_{AM} &= lr_{LM} + m + cr_{MB} \\
r_{AB} &= lr_{LB} + mr_{MB} + c
\end{aligned}
$$

The values of these path coefficients together with the coefficients of correlation from which they were calculated are given in table II.[5] In testing the influence of previous days rainfall on maximum stream height and previous days stream height on weir count the analysis was carried back to the third day, or 72 hours previously. The results showed that the influence of these factors 48 and 72 hours previously was negligible, this being due, as will be shown later, to the rapid run-off in the watershed and likewise in the stream.

TABLE II. *Correlation and path coefficients between daily rainfall, stream level and upstream movement of the salmon (weir count) at McClinton Creek, British Columbia, in 1932 and 1934.*

Correlation between	1932		1934	
	$r \pm \sigma_r$	P_r	$r \pm \sigma_r$	P_r
U and A	0.432 ±0.132	<0.01	0.563 ±0.098	<0.01
U and B	0.754 ±0.071	<0.01	0.746 ±0.064	<0.01
U and L	0.319 ±0.146	0.04	0.416 ±0.118	<0.01
U and M	0.749 ±0.072	<0.01	0.740 ±0.065	<0.01
A and B	0.264 ±0.153	0.10	0.429 ±0.118	<0.01
A and L	0.839 ±0.048	<0.01	0.888 ±0.030	<0.01
A and M	0.218 ±0.157	>0.10	0.479 ±0.111	<0.01
B and L	−0.041 ±0.164	>0.10	0.152 ±0.141	>0.10
B and M	0.839 ±0.048	<0.01	0.888 ±0.030	<0.01
L and M	−0.062 ±0.164	>0.10	0.240 ±0.136	0.09
Path between	$p \pm \sigma_p$	P_p	$p \pm \sigma_p$	P_p
U and A (a)	0.250 ±0.102	0.02	0.298 ±0.095	<0.01
U and B (b)	0.688 ±0.081	<0.01	0.619 ±0.082	<0.01
A and B (c)	0.243 ±0.083	<0.01	0.257 ±0.065	<0.01
A and L (l)	0.854 ±0.047	<0.01	0.837 ±0.033	<0.01
A and M (m)	0.068 ±0.085	0.43	0.050 ±0.078	0.53

U: Number of upstream migrants (daily weir count).
A: Maximum stream level any day during upstream migration.
B: Maximum stream level 24 hours previous.
L: Rainfall any day during upstream migration.
M: Rainfall 24 hours previous.
For schematic illustration of the interrelationships and paths of influence between these factors see diagram on page 160.
P_r: A coefficient of correlation whose probability value (P_r) is less than 0.05 is considered statistically significant; one whose value is greater than 0.05 is not considered statistically significant.
P_p: A path coefficient whose probability value (P_p) is less than 0.05 is considered statistically significant; one whose value is greater than 0.05 is not considered statistically significant.

In the analysis of the interrelationships between these factors it was assumed that rainfall does not directly affect the upstream migration of the salmon but only indirectly through its influence on the stream. The coefficients of correlation between daily rainfall and daily weir count were calculated but have been used, as will be shown later, only to test the adequacy of the qualitative scheme set-up in the above causal factor diagram.

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[5] The use of the coefficient of correlation and the path coefficient based upon it assumes that a linear relationship existed between the variables from which the coefficient of correlation was derived. That is, it implies that a given change in one variable always involved a certain constant change in the corresponding average value of the other. Since the regression between variables is not always linear, it is advisable to check its departure from linearity when using the coefficient of correlation to measure the degree of covariation between the variables. A method for testing the departure from linearity is given by Fisher ('30) page 219. The relationships measured by the coefficients of correlation given in table 2 were tested by this method and found to be linear.

EFFECT OF RAINFALL ON STREAM LEVEL

In the fall of the year when the salmon are migrating into McClinton Creek it usually rains frequently and the surrounding watershed becomes saturated. Under such conditions a shower of less than one inch of rain will cause a rapid rise in the stream within a few hours. After a heavy shower during periods of frequent rains the water drops fairly rapidly to a level of approximately 4 feet and rather slowly thereafter. A somewhat different set of conditions may exist in the stream when periods of frequent rain alternate with more or less extended dry periods. After a dry period as much as one inch of rainfall within a day is required to saturate the watershed and cause a noticeable rise in the stream level. The daily rainfall at McClinton Creek and its maximum daily water height in the fall of 1932 and 1934 are shown graphically in figure 5.

The rapid rate of run-off in McClinton Creek and its watershed is indicated by the low values of m and c which measure the direct influence of rainfall (M) and stream level (B) 24 hours previously on stream level (A) today. The values of m^2 and c^2 given in table III may be used as a measure of the quantitative influence of these factors on stream level (A). Hence less than 1 per cent of the total variation in stream level (A) was due to the influence of rainfall 24 hours previously and approximately 6 per cent was due to the influence of stream level 24 hours previously.

The direct quantitative influence of rainfall (L) the same day on stream level (A) as measured by l^2, see table III, was 73 per cent in 1932 and 70 per cent in 1934.

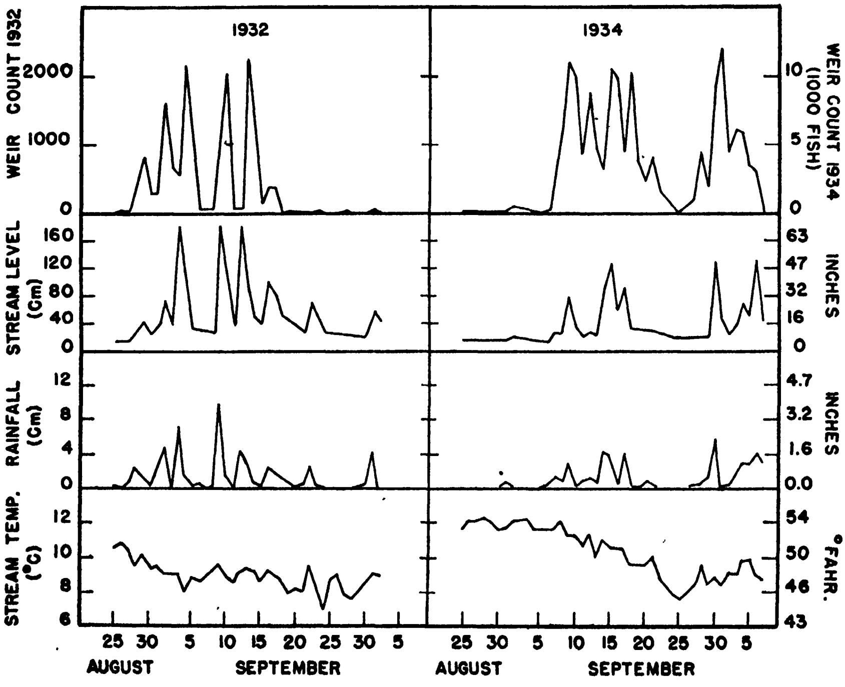

FIG. 5. Daily average stream temperature, daily rainfall, daily maximum stream level and number of pink salmon (daily weir count) migrating into McClinton Creek, British Columbia, in 1932 and 1934.

The total quantitative influence of the three factors L, M and B on stream level (A) may be represented by the term $d_{A(LMB)}$ and calculated from the following equation:
$d_{A(LMB)} = d_{AL} + d_{AM} + d_{AB} + d_{A\overline{LMB}}$
where $d_{A(LMB)} = R^2_{A(LMB)}$, or the total determination of L, M and B on A; $d_{AL} = l^2$; $d_{AM} = m^2$; $d_{AB} = c^2$; and $d_{A\overline{LMB}} = 2lmr_{LM} + 2lcr_{LB} + 2mcr_{BM}$. The value of $d_{A(LMB)}$, see table III, for 1932 was 80 per cent and for 1934 was 88 per cent. Thus the greater part of the total variation in maximum stream height in McClinton Creek during the fall of these years was due to the influence of the variations in rainfall (L) the same day and rainfall (M) and stream level (B) the day before.

TABLE III. *The percentage of the daily variation in stream level and weir count at McClinton Creek in 1932 and 1934 due to the individual, combined and total influences of the factors affecting them.*

Factor		Percentage daily variation in stream level	
		1932 Per Cent	1934 Per Cent
Rainfall same day	$d_{AL} = l^2$	72.9	70.0
Rainfall 24 hour previous	$d_{AM} = m^2$	0.5	0.3
Stream level 24 hours previous	$d_{AB} = c^2$	5.9	6.6
Combined effect of rainfall and stream level	$d_{A\overline{LMB}}$	0.4	10.8
Total effect of rainfall and stream level	$d_{A(LMB)}$	79.7	87.7
Total effect of factors other than rainfall and stream level	d_{AY}	20.3	12.3
Total effect of all factors	$d_{A(LMBY)}$	100.0	100.0
		Percentage daily variation in weir count	
Stream level same day	$d_{UA} = a^2$	6.3	8.9
Stream level 24 hours previous	$d_{UB} = b^2$	47.3	38.3
Combined effect of stream level	$d_{U\overline{AB}}$	9.1	15.8
Total effect of stream level	$d_{U(AB)}$	62.7	63.0
Total effect of factors other than stream level and those associated with it	d_{UX}	37.3	37.0
Total effect of all factors	$d_{U(ABX)}$	100.0	100.0

Since $d_{AY} = 1 - d_{A(LMB)}$, 12 and 20 per cent of the daily variation in stream level during the fall of these years may be attributed to factors not directly associated with immediate rainfall in the watershed. These factors as previously mentioned are believed to be the result of underground drainage. In view of this analysis, it is obvious that the water level in streams of this type may fluctuate widely within a 24 hour period and that the amount of rainfall within the period is primarily responsible for it.

EFFECT OF STREAM LEVEL ON WEIR COUNT

When the rainfall at McClinton Creek amounts to 2 inches or more daily, extreme freshets occur and as the water level approaches 3.6 feet the current becomes too strong for many of the pink salmon to swim against it. At water levels exceeding 4.4 feet the salmon tend to remain in the back eddies out of the main current. As the water level recedes and approaches 3.6 feet, the upstream movement of the salmon becomes more active again. However, since freshets of this magnitude do not occur very frequently and the high water conditions associated with them last only for a few hours at a time, this inhibitory effect of current on the upstream movement of the salmon is not extensive enough to seriously detract from the otherwise linear regression between stream level and weir count (see footnote 5). The daily weir counts of pink salmon into McClinton Creek in 1932 and 1934 are given graphically in figure 5 along with the average daily stream temperatures, the maximum daily water heights, and the daily rainfall during the migratory periods in each of these years.

The correlation and path coefficients between daily weir count and stream level (maximum daily stream height) given in table II indicate that a statistically significant and positive covariation exists between these variables. Since the current of a stream varies so closely with its volume, the covariation between weir count and stream level may have been due as much to the influence of the velocity as to the volume of the water upon the upstream movement of the salmon. It is a matter of common observation that the salmon have a very strong positive reaction to current although it may completely inhibit their upstream movement at very high velocities.

In considering the biological influence of stream flow upon the upstream movement of the salmon, it is necessary also to consider the influence of other factors associated with it, such as the physico-chemical properties of the water. The coefficients of correlation between stream temperature and weir count were negligible thus indicating that fluctuations in the temperature of the water, as in Sashin and Snake Creeks, had no measurable influence on the upstream movement of the fish. Daily variations in the oxygen content and also in the carbon dioxide content (pH values) determined in a recent study (summer of 1940) likewise appeared to bear no appreciable relationship to the daily variations in the weir count. In spite of the absence of any covariation between these factors and weir count, the authors hesitate to assume that the covariation between stream flow and weir count was due wholly to the influence of the volume and current of the water. However, it is believed that any unknown properties of the water in the stream which may have had an appreciable influence on the salmon, were so closely related to its volume that the percentage of variation in the daily weir count related to the daily variations in stream level may be used as a quantitative index of the total causal relationship involved. Chamberlain ('07) in studying the upstream movement of the salmon in Alaska stated "It is well known that in dry seasons, when the streams are low, even though a sufficient depth for a practicable ascent may remain, schools tarry in the bays much longer than in rainy seasons. But as this is marked only in the case of small streams the main factor must be volume or quantity of water."

Those portions (percentages) of the daily variation in the upstream movement of the salmon directly related to the daily variations in stream flow (volume and current) are given by the squared path coefficients a^2 and b^2 reported in table III. The values of these coefficients indicate that in 1932 and 1934 6 and 9 per cent of the daily variation in weir count was due to the variations in stream flow the same day and 38 and 47 per cent was due to variations in stream flow the day before. This lag in the influence of stream flow may be attributed for the most part to the extended influence of the flood waters, following heavy freshets, upon the upstream movement of the salmon. As the flow of McClinton Creek increases the volume of fresh water distributed in the bay likewise increases and its influence extends far beyond the immediate mouth of the stream. Since the salmon upon their arrival from the sea usually become more or less distributed in the bay, larger numbers are subjected to the influence of fresh water following heavy freshets than during periods of decreased stream flow when its influence does not extend much beyond the mouth of the stream. Owing to the rather gradual distribution of the fresh water in the bay, following a freshet, its effect upon the greater body of salmon present would not show in the weir count until the day following the freshet. From an inspection of the graphs in figure 5 it will be seen that the largest daily weir counts usually followed the days upon which the heaviest freshets occurred.

The total percentage of the variability in daily weir count due to the variations in stream flow the same day and 24 hours previously may be calculated from the formula:

$$d_{V(AB)} = d_{VA} + d_{VB} + d_{V\overline{AB}}$$

where $d_{U(AB)} = R^2_{U(AB)}$ or the total determination of A and B on U; $d_{UA} = a^2$; $d_{UB} = b^2$; and $d_{U\overline{AB}} = 2abr_{AB}$. This equation gives a value of 0.63 for both the 1932 and 1934 data (see Table III). In other words 63 per cent of the daily variation in upstream movement of the salmon may be attributed to the variations in the stream flow and its associated factors the same day and 24 hours previously.

In the causal factor diagram the symbol X was used to indicate the influence of factors not associated with stream flow on the upstream migration of the salmon. One factor in this category that appears to be of importance is the degree of sexual development of the salmon. It has been observed at McClinton Creek and likewise in a number of similar streams in southeastern Alaska that if there is insufficient flow in the streams to provide for the ready ascent of the salmon they will remain in the bays until sexually mature. However, upon attaining sexual maturity they will attempt to enter the streams regardless of the flow of water in them. Since the salmon can reach the weir at McClinton Creek even in stages of low water due to its close proximity to the mouth of the stream, sexually mature fish could readily pass through it although the stream flow might not be favorable to their ready ascent to the spawning grounds. Owing to the difficulty of securing adequate quantitative data on the variations in this factor, its effect on weir count cannot be measured directly. However, its influence may be estimated along with that of other unknown factors through the portion (percentage) of variation remaining in daily weir count after that part due to the influence of stream flow has been accounted for. Therefore $d_{UX} = 1 - d_{U(AB)}$. The value of d_{UX}, given in table III, is 37 per cent for both 1932 and 1934. Although all of this residual variation in daily weir count cannot be attributed to the influence of sexual development it is no doubt responsible for a considerable part of it.

If the quantitative scheme set-up in the causal factor diagram on page 160 adequately represents the relationship between the factors then the observed correlations between rainfall and weir count should agree reasonably well with the calculated correlations as determined from the path coefficients between rainfall and stream level and stream level and weir count. The calculated correlations were determined from the following equations:

$$r_{UL} = al + br_{LB} + acr_{LB} + amr_{LM}$$
$$r_{UM} = br_{BM} + am + acr_{BM} + alr_{LM}$$

They are not equal to the observed correlations but with the exception of r_{UL} in 1932, the differences between them range from 6 to 16 per cent of the observed values.

DISCUSSION

The physiographical and physicochemical characteristics of Sashin and Snake Creeks are very much alike. Both streams originate in mountain lakes and have snow fields in their watersheds. Both streams also maintain flows great enough for the salmon to enter them at all times during their inshore migratory period. High falls likewise occur in both streams at the upper limits of the spawning areas which completely aerate the water flowing over these areas. Although there is no falls at the mouth of Sashin Creek, as there is at the mouth of Snake Creek, the water tumbles into the bay over a series of short rapids when the tide is low. These rapids completely disappear, however, at high tide. In spite of the similarity in the origins and environmental conditions in these streams, the pink salmon remain in the bay at Little Port Walter until they are sexually mature before they attempt to enter Sashin Creek, whereas they migrate readily into Snake Creek soon after their arrival in the bay at Olive

Cove, regardless of their state of sexual development. Therefore, since it is very unlikely that this difference in the upstream migrations of these salmon is due to a difference in the character of the streams, it may be due to a difference in their inherent or instinctive behavior. Furthermore the frequent occurrence of both of these types of upstream migration in apparently similar streams leads to such a hypothesis.

Child ('24) describes the origin of instinctive behavior patterns and the conditions responsible for their expression in the organism as follows: "These behavior patterns are among those determined in the individual by the hereditary protoplasmic constitution and the normal or standard range of environmental factors. They represent complex integrations of significance in the life of the individual and so apparently adaptive. In general, however, this instinctive pattern remains merely a potentiality in the behavior of the individual until a particular physiological state arises, either by the attainment of a certain stage of development or by a particular configuration of environmental factors, and determines its realization as an actual reaction pattern. In most, if not in all cases, the environmental configuration plays some part in initiating the actual integration of the instinct pattern into a reaction." Therefore, the inherent behavior pattern of the pink salmon of Sashin Creek that is responsible for the type of their upstream migration depends upon the attainment of a certain state in their development, sexual maturity, for the initiation of the physiological processes that bring about its realization. The salmon of Snake Creek and McClinton Creek, on the other hand, depend upon a particular configuration of environmental factors, state of flow in the streams, for the activation of the inherent behavior pattern that is responsible for the type of upstream migration they usually follow. The stream flow in Snake Creek is favorable to the upstream movement of the salmon at all times except during heavy freshets whereas the flow in McClinton Creek becomes unfavorable under certain conditions of both high and low water. Hence the expression of this behavior pattern in the McClinton Creek salmon is dependent to a great extent upon the state of flow in the stream. Upon the attainment of sexual maturity, however, the salmon of both Snake and McClinton Creeks develop a behavior similar to that of the Sashin Creek fish and attempt to enter the streams regardless of the state of flow. Therefore, it appears that the behavior pattern responsible for the type of upstream migration followed by the Sashin Creek fish is inherent in all of the pink salmon and upon their attainment of sexual maturity is likewise dominant to the behavior pattern that is responsible for the type of upstream migration followed by the Snake and McClinton Creek fish under usual conditions. This basic behavior pattern is essential to the perpetuation of the species for it stimulates the fish to enter the streams at sexual maturity and attempt to spawn regardless of the hazards involved.

Since behavior patterns of this kind are adaptive it would be interesting to speculate on the evolutionary origin of these two types. There are some indications of the manner in which they may have originated but more data must be collected before a hypothetical explanation may be made.

SUMMARY

The influence of stream flow and certain physico-chemical properties of the water upon the upstream movement of the pink salmon is described in three streams, two in southeastern Alaska and one in British Columbia.

Sashin Creek at Little Port Walter, Alaska, originates in mountain lakes and maintains a flow great enough to permit

the entrance of the adult salmon at all times during their inshore migration. The salmon, however, do not migrate directly into Sashin Creek upon their arrival at Little Port Walter, but mill about in the bay until sexually mature before they attempt to enter it. The first salmon to arrive in the bay become sexually mature about the middle of August at which time they school up at the mouth of the stream and move into it. Once the salmon have collected at the mouth of the stream preparatory to entering it they may react favorably to sudden changes in its flow. There appears to be no appreciable relationship between variations in stream temperature and the upstream movement of the salmon.

Snake Creek at Olive Cove, Alaska, also originates in mountain lakes and likewise maintains a flow great enough for the adult salmon to enter it at will. An entirely different type of upstream migration, however, occurs in this stream. The pink salmon move directly into Snake Creek a few days after their arrival at Olive Cove and collect in a quiet stretch of water in the stream, a short way above its mouth, where they remain until sexually mature and ready to spawn. A 10-foot falls occurs at the mouth of Snake Creek and during extreme freshets it becomes almost impassable to the salmon, otherwise there is no appreciable influence of stream flow upon their upstream movement. No appreciable relationship appears to exist between the variations in the temperature or carbon dioxide (pH) contents of the water and the upstream movement of the salmon.

McClinton Creek at McClinton Bay, British Columbia, originates in mountain slopes and has practically no storage capacity in its watershed. Its flow during the inshore migration of the salmon depends almost entirely upon surface run-off and is therefore closely related to the daily rainfall. If the water level is up and showers occur from day to day the pink salmon will migrate directly into the stream shortly after their arrival in the bay. They move upstream readily, except during extreme freshets, and congregate in deep holes where they remain until sexually mature and ready to spawn. If, on the other hand, the water level in the stream is low and clear weather continues the salmon will mill about in the bay until it rains and the stream rises. This reaction of the salmon to low water conditions in the stream will continue until they become sexually mature at which time their reaction changes and they attempt to enter the stream regardless of its water level. Hence the pink salmon at McClinton Creek normally follow the Snake Creek type of upstream migration but may change over to the Sashin Creek type under certain environmental conditions.

The interrelationship between the various environmental factors and their influence upon the upstream movement of the salmon was tested statistically by means of correlation and path coefficient analyses.

The distinct difference in the type of upstream migration occurring at Sashin Creek and Snake Creek cannot be attributed to a corresponding difference in the character of the streams and is believed to be due to a difference in the inherent or instinctive behavior patterns of the salmon. Furthermore, in view of the change made by the salmon at McClinton Creek, under certain conditions, from the Snake Creek to the Sashin Creek type of upstream migration, it appears that the Sashin Creek behavior pattern is basic in all of the pink salmon and dominant upon their attainment of sexual maturity.

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A STUDY OF THE ROOTS OF *BROMUS INERMIS* IN RELATION TO DROUGHT RESISTANCE[1]

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INTRODUCTION

In the semi-arid regions of the West where moisture generally is considered the most important factor limiting growth, a plant must be drought resistant[2] in order to ecize and become of economic value. Factors affecting drought resistance are many and variable but, generally, they can be classified as those enabling a plant (1) to withstand desiccation or (2) to prevent desiccation. The latter can be effected by reducing water loss or increasing efficiency of water intake. Efficiency of water intake has received relatively little attention from scientists. Because of its importance, a study of root development characteristics of selections of smooth bromegrass (*Bromus inermis* Leyss.) was initiated. General observations have suggested that a knowledge of root systems may do much to explain differences in drought resistance displayed by plants.

Smooth bromegrass was selected for this study because of extensive previous experimental work on this species. It is drought resistant, highly palatable, and a high yielder of seed and forage. Likewise, it displays great diversity in leafiness and growth habit; many individuals are erect and close growing, while others spread vigorously by rootstocks. Because of the wide variation among individual plants, bromegrass lends itself well to experimental selection. The purpose of this investigation was to study the normal developmental differences in root and top growth among selections exhibiting differences in ability to withstand controlled artificial drought in the seedling stage, in an effort to determine the role of root and top development in bringing about drought resistance.

LITERATURE REVIEW

Many methods have been devised for studying varietal selections to determine relative drought resistance. These include general field observation, chemical analysis, rate of transpiration, and physiological and anatomical analysis (Maximov, '29; Newton and Martin, '30). Probably the most satisfactory, however, is the controlled artificial drought test (Aamodt, '35; Bayles *et al.*, '37; Hunter *et al.*, '36; McAlister, '40; Schultz and Hayes, '38). This method is still in its incipient stages of development and is subject to the criticism that it ignores extent and, especially, depth of the root system. Nevertheless, the procedure for certain types of forage plants has become rather well established and, in some cases, high correlation has been found between these tests and field observation.

Root studies as an index to drought resistance are limited in number, and deal only with established varieties. Collins ('14) reported from his studies on drought-resistant strains of maize that the seedlings of the hardy varieties lacked secondary root branches entirely and the roots extended to a greater depth than did non-hardy varieties. Hubbard ('38) concluded that extensive root branching of the drought-hardy varieties was responsible for their greater yields during drought periods.

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[1] The author wishes to acknowledge his sincere appreciation to Dr. L. A. Stoddart for efficient direction and encouragement throughout the study, and to Dr. D. F. McAlister for materials and photographic work.

[2] The term "drought resistant" is not used in the strict interpretation of Shantz ('27), but as Maximov ('29) expresses it; the capacity of plants to endure soil drought, atmospheric drought, or a combination of both and to recover readily after permanent wilting without dangerously hindering the development of the plant.

Weaver ('19), Pavlychenko ('37), and Albertson ('37) emphasized the importance of depth and extent of root systems in enabling plants to develop normally under adverse moisture conditions. Ivanov ('23) also demonstrated this fact by his classical work on drought-resistant plants in which he stated that the ability of a plant to resist drought is directly proportional to density and extent of the root system. Noll ('39) reported that during periods of extreme drought, shallow-rooted wheat plants died, those of moderate depths suffered greatly and only deeply rooted plants functioned normally.

General root studies dealing with smooth bromegrass (Love and Hanson, '32; Sheppard, '05; Ten Eyck, '00) yielded the interesting observations that its roots penetrated to a depth of almost eight feet and produced one of the densest root growths of the numerous grasses studied. However, none of the studies on this species shows the progressive development of the roots during the first year of growth.

Newton and Martin ('30) and Maximov ('29) presented excellent comprehensive reviews on factors affecting drought resistance among plants but failed to emphasize the important role that roots play as a factor in the resistance.

Experimental Methods and Growing Conditions

Seeds of eight bromegrass selections were obtained from the Division of Forage Crops, Bureau of Plant Industry at Logan, Utah. These selections had been tested for drought resistance under conditions of controlled soil drought and found to show differences in their abilities to withstand drying in the seedling stage. Four tested significantly high, three significantly low, and one was intermediate. The experimental number and drought resistance data for the eight selections as determined by the Bureau of Plant Industry in terms of percentage survival are shown in table I.

Table I. *Average percentage survival of* Bromus inermis *selections in controlled soil drought tests. Data from McAlister (unpublished)*

Experimental number*	Bureau of Plant Industry selection No.	Survival			Average survival
		(per cent)	(per cent)	(per cent)	(per cent)
H-1	Neb. 1678D	76.8	66.7	66.4	70.0
H-2	Neb. 96-23C	70.1	59.4	52.2	60.6
H-3	Utah 02	—	—	61.0	61.0
L-4	Wash. 38PR151	17.3	20.7	—	19.0
L-5	Canada 125783 (Parkland)	40.6	27.4	40.7	36.2
H-6	Neb. 90-1706	74.6	64.2	45.0	61.3
L-7	Wash. 38PR187	—	—	29.0	29.0
M-8	Neb. 96-20D	60.4	37.9	59.4	52.9
Difference necessary for significance at the .05 point.......		20.2	20.2	15.7	

* H, L, and M indicate high, low, and medium drought-resistance ratings according to Bureau of Plant Industry experimental data.

On March 29, 1941, plantings were made at the Utah State Agricultural College Experimental Farm, two and one-half miles north of Logan, Utah. The plot produced a crop of barley the previous year and was plowed in the late fall of 1940 after the crop was removed. In the spring of 1941, it was thoroughly harrowed and, thereafter, received no cultivation other than an occasional weeding. The seeds were planted in a randomized block, with two replications. They were spaced in rows 40 inches apart and thinned to one plant every 40 inches within the rows. Each row contained 45 individual plants.

Climate. The mean annual precipitation at Logan, over a period of ten years, 1930–40, was 15.53 inches. Approximately 40 per cent fell as snow from November to March. The remainder was received as rain, most of which fell in the spring and autumn, approximately 29 per cent and 19 per cent respectively, leaving 12 per cent for the three summer months of June, July, and August.

The average maximum and minimum temperatures for July and August from 1930–40 were approximately 86 degrees and 58 degrees Fahrenheit respectively. Maximum temperatures above 100 degrees for several consecutive days were not uncommon during the summer months. Winds of high velocity were rare.

Cool weather marked the beginning of the growing season of 1941. The soil contained adequate moisture and the air was humid during the early spring months. Growing conditions, in general, were better than normal throughout the entire experimental period. They were marked by precipitation well above the average for the ten previous years. The average precipitation in each water year for the period 1930–40 was 15.53 inches as compared to 19.13 inches for the water year 1940–41.

The plants received no irrigation water throughout the entire period. Despite this, unusually heavy precipitation kept the soil plentifully supplied with moisture as shown in table II.

TABLE II. *Per cent of available * soil moisture on experimental plot*

Depth	April 27	June 5	July 7	July 31	Sept. 10	Oct. 17
	(per cent)	(per cent)	(per cent)	(per cent)	(per cent)	(per cent)
6″	13.1	10.0	8.8	10.4	6.0	14.6
1′	13.4	8.6	6.8	4.6	6.1	4.5
2′	7.4	4.0	10.6	6.3	5.8	9.3
3′	6.4	7.7	3.1	6.8	5.8	6.1
4′	9.5	11.0	8.0	6.5	5.4	6.1
5′	8.5	9.4	8.4	7.8	6.6	6.6

* Per cent above hygroscopic coefficient.

Brief hot and rainless periods during the summer were not uncommon. Nevertheless the average maximum and average minimum temperatures for the three summer months indicate favorable temperatures for normal growth. For the three summer months, June, July and August of 1941 the average maximum and average minimum temperatures were 75°, 86°, 82°, and 51°, 60°, 58° respectively.

Soil. The soil is a Millville loam of comparatively recent origin from an alluvial fan. The surface 14 inches is a dark-brown friable loam, highly calcareous and easily penetrated by roots. From 14 to 36 inches it is a loam, massive in structure, highly calcareous, and light brown in color. From 36 to 60 inches there is a fine sandy loam to fine sand, compact in structure, and light brown to grayish brown in color.

Isolation of the root system. The roots were isolated by a modification of the method devised by Pavlychenko ('37), known as the block excavation method. Briefly, it consists of the isolation of a prism of soil around the plant, large enough to contain the entire root system. The prism is then enclosed tightly by means of a solid frame and the column of soil is hoisted out of the pit by means of a derrick. The block is soaked in water for several hours in a large tank with one side of the frame removed. The water is then drained from the tank and the soil washed from the roots by a water spray after which the roots and tops are placed in a small tank with sufficient water to submerge the roots entirely when spread out horizontally along the bottom. Here they are measured and studied before being mounted in their natural position according to field notes. The mounting is done by placing a large blotter under the plant while it is submerged in water. Then by gently lifting the top edge of the blotter the roots can easily be guided into their natural position on the blotter. They are allowed to dry partially and, later, are pressed. Thereafter, they can be removed as many times as desired for photographing and study without serious injury to any portion of the plant (figure 1).

FIG. 1. A single root system of smooth bromegrass at 12 weeks of age displaying detail procured by the block excavation method (1/6 natural size).

Number of plants studied and measurements taken. Three plants from each of two replicated rows constituted a sample for each strain at each extraction date, making a total of six plants studied for each of the eight strains. In all, 48 plants were dug at each of six dates: May 16, June 1, June 15, July 5, August 7, and October 12, at which times the ages of the plants were 5 weeks, 7 weeks, 9 weeks, 12 weeks, 16 weeks, and 6 months respectively.

The following counts and measurements were made for each plant excavated: total number of roots; average depth of root penetration, excluding branches (average of all roots measured from soil surface to tip of root); average maximum depth of root penetration (average of values of the deepest root for each plant sampled); total axial length of roots (main axial length excluding branches, measured from origin on stem to tip of root); total number of stems; average height of stems (measured to tip of terminal leaf); total axial length of all stems; average weight of roots; average weight of tops; and top weight to root weight ratio. The counts and measurements in every case were studied for dependability by analysis of variance and interpretations were made by the use of Fisher's "T" test (Fisher, '36).

RESULTS

The results procured show interesting differences that are believed to be important in evaluating the drought resistance of smooth bromegrass selections and a brief summary of the data is presented.

Extent of root growth

The root systems of the eight selections studied varied widely in extent and rate of growth during the six months that they were under observation. Some grew rapidly throughout the entire season, some made rapid early growth, but grew slowly during the middle or latter part of the season, while still others made their most pronounced growth late in the season.

Two types of roots were found in smooth bromegrass. One type was slightly larger in diameter than the other and of a lighter color. These roots were produced only from tillers and rhizomes. The second type was smaller in diameter, darker colored, and more extensively clothed with hairs. This latter type of root arose from the sub-crown internode and from the first crown node and made up the major portion of the root system. These "small" roots extended downward from two to three times the depth of the "large" roots and produced a dense network of fine branches. The primary roots were measured and counted as the smaller type since they were indistinguishable after a few weeks of age.

Numbers H-1 and H-6, in most cases, displayed characteristics that would lead an observer to choose them as the two most drought resistant selections, and numbers L-5 and L-7 appeared to be the least drought resistant. Therefore, these four were considered representative of resistant and non-resistant selections.

Lateral spread of roots. The differences in lateral spread of roots were found to be related to rhizome production; hence plants producing the largest numbers of rhizomes at an early date consequently had greatest lateral spread. Strains of *Bromus inermis* are known to vary greatly in rhizome production, some being of the "bunch" type and some the spreading or sod-forming type. Though definite conclusions are impossible from data on young plants, H-1 appeared to be a "bunch" type because of shortness of rhizomes and L-5 because of lack of rhizome production. In any event, these two selections had a lesser lateral root spread than did the other six strains. At no time during the study were there any significant differences in lateral spread of roots between the hardy and non-hardy groups.

Average maximum depth of roots. Deeply penetrating roots are believed desirable for drought resistance as emphasized by Collins ('14), on studies with Hopi maize. In the present study, selection H-6 varied in depth from 10.5 inches at 5 weeks of age to 53.3 at 6 months of age as contrasted with L-5 which varied from 8.7 inches at 5 weeks to 27.5 inches at 6 months of age (table III). Numbers H-1 and H-6, in most cases, had roots significantly deeper than L-5 and L-7.

Average maximum depth of "large" roots yielded relatively little information and was not considered a reliable index to drought resistance. Their depths were not found to differ significantly on the last date the plants were examined (table IV).

TABLE III. *Average of six root systems of eight* Bromus inermis *selections planted March 29 and excavated at various dates*

Age of plants*	5 wks.	7 wks.	9 wks.	12 wks.	16 wks.	6 mons.
Date	May 16	June 1	June 15	July 5	Aug. 7	Oct. 12
Average Number of "Small" Roots Per Plant						
H-1	4.5	4.9	7.3	12.3	25.6	51.2
H-2	2.6	2.9	5.4	16.0	24.0	38.6
H-3	3.3	3.9	5.7	25.3	27.3	42.2
L-4	2.6	3.8	6.0	19.6	21.3	24.7
L-5	4.0	4.0	8.5	10.5	14.0	30.7
H-6	4.3	4.6	6.4	12.8	20.3	45.6
L-7	2.5	2.8	4.7	8.4	19.0	30.2
M-8	4.5	3.9	5.4	10.4	20.6	31.2
†Sig. Diff.	1.0	.7	.9	2.9	2.3	6.0
Average Maximum Depth of "Small" Roots Per Plant in Inches						
H-1	8.9	9.2	16.9	21.1	32.7	34.5
H-2	12.5	10.5	14.4	23.0	29.2	41.3
H-3	10.3	8.9	14.0	21.8	36.3	32.7
L-4	9.0	5.5	12.0	20.8	25.3	26.5
L-5	8.7	9.2	10.8	17.9	20.3	27.5
H-6	10.5	8.6	14.6	19.4	34.4	53.3
L-7	7.9	9.2	11.2	14.2	26.3	28.2
M-8	8.8	8.7	14.2	19.0	27.6	34.2
†Sig. Diff.	1.3	1.2	1.6	2.3	5.5	8.3
Average Depth of "Small" Roots Per Plant in Inches						
H-1	4.1	9.0	11.1	18.7	16.1	17.8
H-2	8.2	10.5	10.1	13.8	17.4	19.1
H-3	5.9	9.3	9.0	11.9	17.6	18.3
L-4	5.0	5.7	7.7	11.8	12.4	12.3
L-5	4.0	5.0	6.3	9.6	10.5	15.2
H-6	5.7	10.5	9.7	17.1	19.3	18.9
L-7	4.3	5.0	6.4	9.0	15.9	13.7
M-8	4.1	8.0	9.1	8.7	15.9	15.2
†Sig. Diff.	.8	1.4	1.2	2.7	2.8	1.9
Average Total Axial Length of "Small" Roots Per Plant in Inches						
H-1	18.8	44.1	81.0	230.1	412.1	911.3
H-2	21.9	30.4	54.5	221.9	417.6	737.2
H-3	30.4	36.2	47.7	303.3	480.4	774.0
L-4	13.4	21.6	46.2	231.2	264.1	303.8
L-5	16.3	20.1	53.4	100.8	147.0	468.1
H-6	24.9	48.3	62.0	218.8	391.7	863.1
L-7	10.8	14.4	30.0	75.6	302.1	414.4
M-8	18.8	31.2	49.1	90.4	327.5	474.2
†Sig. Diff.	5.0	10.6	6.6	63.2	80.6	89.5

* Calculated from April 9, approximate date of emergence.
† Mean difference necessary to be significant at the .05 point.

The available soil moisture on July 31, at a depth of 12 inches was below 5 per cent. Had the month of August not been favored with showers, these hardy selections displaying an average maximum root depth of 36 inches certainly would have been more capable of supply-

TABLE IV. *Average of six root systems of eight* Bromus inermis *selections planted March 29 and excavated at various dates*

Age of plants*	7 wks.	9 wks.	12 wks.	16 wks.	6 mons.
Date	June 1	June 15	July 5	Aug. 7	Oct. 12
Average Number of "Large" Roots Per Plant					
H-1	3.0	3.7	9.0	9.5	12.6
H-2	2.0	3.0	8.0	10.2	24.6
H-3	2.6	3.5	9.0	10.0	13.2
L-4	2.0	3.2	8.1	9.0	9.5
L-5	2.5	2.5	3.0	5.3	6.5
H-6	3.0	4.2	10.0	15.1	21.0
L-7	1.0	2.3	3.3	8.0	10.7
M-8	3.0	3.5	6.2	9.2	12.2
†Sig. Diff.	.7	1.0	1.6	2.2	3.3
Average Maximum Depth of "Large" Roots Per Plant in Inches					
H-1	5.2	6.1	7.2	14.7	12.2
H-2	4.2	6.5	6.5	14.0	17.3
H-3	4.5	6.1	7.3	17.0	13.2
L-4	2.5	6.5	4.0	10.1	13.2
L-5	3.0	4.5	4.1	7.1	11.0
H-6	5.0	6.9	10.9	20.8	15.6
L-7	4.7	3.0	4.0	14.5	13.2
M-8	4.5	5.1	4.8	12.2	18.0
†Sig. Diff.	.7	1.2	1.3	1.6	Not sig.
Average Depth of "Large" Roots Per Plant in Inches					
H-1	4.0	5.6	3.0	4.0	6.7
H-2	4.1	4.8	3.0	10.2	9.2
H-3	4.2	5.4	4.5	9.8	8.3
L-4	3.1	5.7	1.9	5.7	7.0
L-5	2.0	3.8	3.2	2.2	6.0
H-6	5.0	5.6	6.3	10.4	8.8
L-7	3.2	2.5	1.2	6.4	7.0
M-8	4.0	3.9	1.9	7.5	8.1
†Sig. Diff.	1.3	.8	1.3	1.2	Not sig.
Average Total Axial Length of "Large" Roots Per Plant in Inches					
H-1	12.0	20.7	27.0	50.7	84.4
H-2	8.2	14.4	24.0	104.0	226.8
H-3	10.9	18.9	40.5	98.0	110.2
L-4	6.2	18.2	15.3	51.3	66.5
L-5	5.0	9.5	9.6	11.6	39.0
H-6	15.0	23.5	63.0	157.0	185.6
L-7	3.2	5.7	3.9	51.5	56.7
M-8	12.0	13.6	11.7	69.0	99.0
†Sig. Diff.	5.4	3.9	13.8	26.4	46.2

* Calculated from April 9, approximate date of emergence.

† Mean difference necessary to be significant at the .05 point.

ing the plants with water than the nonhardy selections with only a depth of 24 inches (table III).

Average number of roots per plant. It should be pointed out that in measuring the roots it was impossible after July 5 to trace the individual roots to their stem origins without breaking them because of numerous rhizomes and a network of roots near the crown. Therefore, some roots which appeared to be individuals may have been lateral root branches arising from their parent roots near the latter's point of origin. The plants were not consistent in their addition of roots from date to date. This is comparable to the findings of Walworth and Smith ('18) concerning the variation in the production of secondary roots in cereals. They found that the number was not constant within the strain because of great fluctuations among individuals. Despite this fact, different varieties of a given cereal showed characteristic tendencies in the production of these roots. As shown in tables III and IV, it was found that some bromegrass selections produced a relatively large number of roots in the early season while others added a great number in the middle or latter part of the season. However, the more drought resistant strains, H-1 and H-6, were consistently higher in number of both "large" and "small" roots than were L-5 and L-7.

Average depth of roots per plant. The average depth of the roots is affected profoundly by the addition of new roots; thus, the same variation is found in average depth as was encountered in average number of roots per plant. The average depth of "small" roots varied from 8.25 inches at 5 weeks of age to 19.10 inches at 6 months for the plants having a high drought resistance rating as compared to 4.09 inches to 12.30 inches for the plants rated low. With only two exceptions, H-1 and H-6 had significantly greater average root depths than L-5 and L-7 during the entire season (table III).

The average depth of "large" roots per plant varied a great deal more among selections than did that of "small" roots. Number H-6 was consistently high, varying from 5.0 inches at the first date of excavation to 8.84 inches at the last date. With one exception, L-5 had a lesser average depth of "large" roots at all dates, varying from 2.0 to 6.07 inches. There were no significant differences among the selections at the last date of inspection (table IV).

The average root depth is an expression of the depth and number of roots per plant and yields valuable information for comparing selections for drought resistance. For example, had the atmosphere and the upper 18 inches of soil been dry during July and August, the plants having an average root depth of 20 to 30 inches likely would have been more capable of furnishing water to the plant than would those with an average root depth of 8 to 19 inches, as was the case in the hardy and non-hardy strains of smooth bromegrass during this period.

Average total axial length of roots per plant. The total axial length of roots is, perhaps, one of the most desirable measurements for evaluating a root system. The axial length of the "small" roots of the hardy selections (H-1 and H-6), in all cases excepting the first date of excavation, was significantly greater than that of the non-hardy selections (L-5 and L-7). The length varied from 18.85 inches at 5 weeks of age to 911.36 inches at 6 months for H-1, in contrast with 10.85 inches to 414.42 inches for L-7 (table III).

Total axial length of the "large" roots was highly variable among selections since these roots were produced in direct proportion to the production of tillers and rhizomes. Much less significance is attached to total length of "large" roots as an index to drought resistance than to total length of "small" roots. However, the "large" roots of H-6 were significantly longer than those of the non-resistant selections in all cases, and those of L-5 were significantly shorter than those of the resistant selections at all dates except the last (table IV).

Since axial length is believed to be so reliable as an index to drought resistance, total lengths ("small" roots + "large" roots) were computed and very important differences were found. At each of the five dates as shown in table V, axial root lengths of drought-resistant selections (H-1 and H-6) were significantly greater than those of less resistant selections (L-5 and L-7). At seven weeks of age H-6 had a total axial root length of 63.30 inches and at 6 months of age a total of 1048.80 inches, while H-1 had 56.10 inches at seven weeks of age and 975.01 inches at 6 months of age. The two non-hardy strains produced lengths of only 25.15 and 17.65 inches at seven weeks and 507.62 and 471.17 inches at 6 months respectively.

TABLE V. *Total average axial length of both "small" and "large" roots of six root systems of eight* Bromus inermis *selections planted March 29 and excavated at various dates.*

Age of plants	7 wks.	9 wks.	12 wks.	16 wks.	6 mons.
Date	June 1	June 15	July 5	Aug. 7	Oct. 12
	(inches)	(inches)	(inches)	(inches)	(inches)
H-1	56.1	101.7	257.1	464.8	975.0
H-2	38.6	68.9	245.9	521.6	964.1
H-3	47.2	66.6	343.8	471.1	871.0
L-4	27.9	64.4	246.7	265.3	369.8
L-5	25.1	63.0	110.4	158.7	507.6
H-6	63.3	85.6	381.9	548.8	1048.8
L-7	17.6	35.8	79.6	369.4	471.2
M-8	43.2	62.8	102.3	396.5	573.3
*Sig. Diff.	3.3	7.6	76.6	77.7	89.6

* Mean difference necessary to be significant at the .05 point.

Measurements of foliage

All measurements of foliage were quite variable among the selections as illustrated in table VI. Generally, however, it can be stated that the hardy selections made a more vigorous herbage growth

TABLE VI. *Average counts and measurements on foliage of six plants of eight* Bromus inermis *selections planted March 29 and observed at various dates.*

Age of plants	7 wks.	9 wks.	12 wks.	16 wks.	6 mons.
Date	June 1	June 15	July 5	Aug. 7	Oct. 12
Average Number of Stems Per Plant					
H-1	3.0	6.1	11.0	51.7	122.7
H-2	2.0	3.4	8.2	28.0	122.0
H-3	2.6	4.1	13.0	46.3	96.0
L-4	2.0	4.5	14.0	41.0	51.0
L-5	3.0	6.0	9.4	34.4	74.0
H-6	3.0	4.1	7.8	38.0	132.0
L-7	2.0	2.2	4.1	49.1	96.5
M-8	3.0	5.0	9.2	72.0	109.5
*Sig. Diff.	.8	1.1	1.8	2.5	4.6
Average Height of Stems Per Plant in Inches					
H-1	1.5	4.5	4.6	7.7	7.0
H-2	1.0	3.8	5.2	6.0	5.8
H-3	1.5	3.6	6.1	6.2	5.4
L-4	0.2	4.0	5.9	5.3	4.8
L-5	0.5	0.5	3.7	4.4	5.4
H-6	2.5	3.4	5.0	5.2	6.8
L-7	0.2	1.3	2.8	6.0	5.3
M-8	2.7	4.0	5.2	5.2	5.7
*Sig. Diff.	.2	.6	1.1	.4	1.2
Total Axial Length of Stems Per Plant in Inches					
H-1	4.5	27.7	50.5	399.6	864.4
H-2	1.9	12.6	42.4	172.7	711.4
H-3	3.9	14.9	79.3	287.2	521.2
L-4	.4	17.9	82.4	219.3	248.2
L-5	1.5	3.0	34.2	151.2	403.9
H-6	7.3	14.1	39.1	197.6	901.1
L-7	.4	2.8	11.7	297.5	511.0
M-8	8.0	20.1	47.2	378.9	629.9
*Sig. Diff.	1.2	4.9	5.6	52.2	108.4

* Mean difference necessary to be significant at the .05 point.

throughout the season than did the less hardy.

Weight comparisons of tops and roots

The weight of tops was closely proportionate to the total axial length of stems and a similar relationship existed between weight of roots and total axial length of roots. These relationships can be shown statistically in each case (tables V, VI, and VII). Haber ('38), in a controlled drought test with strains of sweet corn, found no significant differences between weight of roots of susceptible and resistant lines to account for differences in their ability to withstand drought.

It is shown in table VII that there was no significant difference in weights of roots at 9 weeks of age. Other measure-

TABLE VII. *Average dry weight of tops and roots of six plants of eight* Bromus inermis *selections and a comparison of their ratios observed at various dates.*

Age of plants	9 weeks	12 weeks	6 months
Date	June 15	July 5	October 12
Average Weight of Tops Per Plant in Grams			
H-1	.55	1.81	31.04
H-2	.30	1.67	30.69
H-3	.33	2.57	18.71
L-4	.49	3.89	10.11
L-5	.46	.67	14.36
H-6	.58	.98	34.20
L-7	.13	.31	17.49
M-8	.29	1.92	20.03
*Sig. Diff.	Not sig.	.53	Not sig.
Average Weight of Roots Per Plant in Grams			
H-1	.58	2.01	34.03
H-2	.34	1.48	29.73
H-3	.35	2.51	19.15
L-4	.39	2.13	8.83
L-5	.34	.42	11.69
H-6	.65	1.80	35.89
L-7	.12	.27	14.59
M-8	.35	1.73	17.42
*Sig. Diff.	Not sig.	.64	7.58
The Weight Ratio of Tops to Roots			
H-1	.79	.89	.90
H-2	.86	1.18	1.04
H-3	.92	1.02	1.00
L-4	1.29	1.63	1.26
L-5	1.39	1.64	1.21
H-6	.81	.54	.97
L-7	1.02	1.31	1.21
M-8	.89	1.09	1.23
*Sig. Diff.	.29	.37	Not sig.

* Mean difference necessary to be significant at the .05 point.

FIG. 2. Seedlings of *Bromus inermis* as they appeared at 5 weeks of age. Left to right, selections L-7, L-5, H-1, and H-6.

ments on the roots showed significant differences that appear important in the classification of resistant and non-resistant selections. Also, it is shown that at 9 weeks the ratios between top and root weights were significantly different. Numbers H-1 and H-6 had the lowest top-root ratio at all dates (table VII). Weight of individual root systems, alone, will not necessarily be a measure of ability to furnish water to the plant, since coarse roots and fine roots of the same weight may differ in efficiency of procuring water from the soil because of differences in area of absorbing surface. In considering plants of similar root and foliage characteristics, the weight of foliage in proportion to the weight of roots might be an expression of the roots' ability to furnish water to replace the loss of moisture by transpiration. As pointed out by Miller ('16), drought resistance in corn and sorghums was proportional to root development in relation to foliar area. Numbers H-1 and H-6 were, in most cases, significantly different from the non-hardy selections. On the last date of observation, the differences shown were in favor of the resistant selections but were not of sufficient magnitude to be dependable (table VII).

Growth characteristics at different stages

Interesting differences in growth rates and development were found among the eight selections of *Bromus inermis* at each date of excavation. Following is a brief record of the important differences noted.

Five-week old seedlings. At five weeks the plants were about two inches tall and had from two to six unfolded leaves (figure 2). In non-resistant and resistant selections respectively, the roots varied in maximum depth from 7.9 to 12.5 inches and in numbers from 2.66 to 4.50. With the exception of one non-resistant selection, the resistant strains showed a significantly greater total axial root length (table V).

Seven-week old plants. At this stage, the plants were approximately 3.2 inches high and possessed from 1 to 2 tillers. Measurements on foliage and "large" roots showed no consistent differences between high and low drought resistant selections. The average total axial length of the "small" roots at this date showed that three of the drought resistant strains possessed significantly greater lengths than did any non-resistant strain. Selection H-6 had an axial root length of 48.30 inches as contrasted to 20.15 inches for L-7. The hardy selections produced a significantly greater average root depth than did the non-hardy. Numbers H-1 and H-6 possessed roots that reached an average depth of 9.0 and 10.5 inches respectively as compared to L-5 and L-7 each of which reached but 5.0 inches (table III). As shown in table V, the resistant strains at seven weeks had a significantly greater total axial length of all roots than did the non-resistant selections, without exception.

Nine-week old plants. At this stage, the plants possessed an average of 4.5 stems which had reached an average height of 4.5 inches (figure 3). It is shown in table III that all measurements on "small" roots, excepting one, are significantly greater for the resistant selections (H-1 and H-6) than for the non-resistant selections (L-5 and L-7). The "large" roots at this date did not differ consistently between the high and low drought resistant strains (table IV). The total axial length of all roots of H-1 and H-6 was significantly greater than that of any non-resistant strain (table V). As shown in table VII, the ratio of top to root weight was significantly higher in all non-resistant strains, with the exception of L-5.

Twelve-week old plants. The 12-week plants were approximately 6 inches high and had an average of 10 stems per plant. The linear measurements on "small" roots at this period show differences between the non-resistant and the resistant selections that are consistent throughout. The roots of the four high-rated strains are consistently longer and deeper than are those of any of the four poorer selections (table III). The four drought-resistant strains possessed significantly greater total axial length of "large" roots than did L-5 and L-7. All other measurements on "large" roots showed only a tendency to favor drought-resistant strains (table IV). The drought-resistant selections (H-1 and H-6) produced a significantly longer total axial root length than did non-resistant strains (L-5 and L-7) as shown in table V. At this stage of growth (table VII), H-1 and H-6 were significantly different from L-5 and L-7 in all weight measurements. Selections H-1 and H-6 not only yielded a greater weight of both roots and tops than did L-5 and L-7 but were found to produce significantly greater amounts of roots in proportion to the foliage.

Sixteen-week old plants. At 16 weeks, the plants were about 9 inches high and had an average of 45 stems per plant (figure 4). All the measurements taken

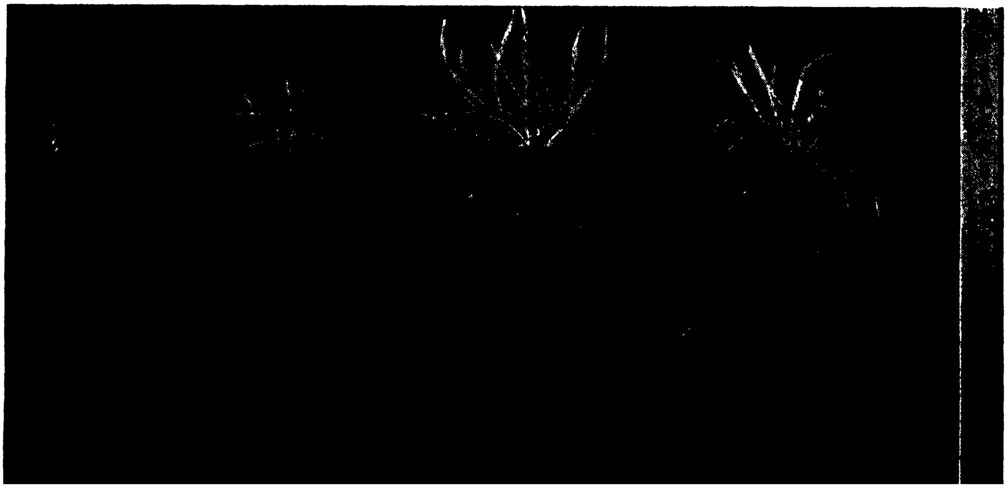

FIG. 3. Plants of *Bromus inermis* as they appeared at 9 weeks of age. Left to right, selections L-7, L-5, H-1, and H-6.

FIG. 4. Plants of *Bromus inermis* as they appeared at 16 weeks of age. Left to right, selections L-7, L-5, H-1, and H-6.

on "small" roots showed the four high-rated strains to be superior without exception (table III). The measurements on "large" roots brought out no consistent differences between the resistant and non-resistant selections. The four hardy selections, however, showed a strong tendency toward greater total axial length of both "large" and "small" roots (table V). Most selections possessed some plants that were in anthesis at this date, but H-1, L-4, and L-5 were materially later than others.

Six-month old plants. At the final observation, most of the plants possessed mature seed heads and their leaves were beginning to turn brown (figure 5). The average number of stems per plant varied from 51 to 132. The roots of the four hardy selections were still superior to those of the three non-hardy in all respects as shown in tables III and IV. The four drought-resistant selections had significantly greater total axial length of both "small" and "large" roots than the three non-resistant. Numbers H-1 and H-6, had a total root length of 975.01 inches and 1048.80 inches respectively as compared to 507.62 inches and 471.17 inches for L-5 and L-7 (table V). The weight of the foliage, and the top weight to root weight ratios were not found to be significantly different; nevertheless, H-1 and H-6 tended toward lower top-root ratios, which would favor drought resistance (table VII). Numbers H-1 and H-6 also possessed significantly greater root weights than did L-5 and L-7.

DISCUSSION

Scientific investigators have long been interested in the ability of certain plants to resist drought and, as a result, a great many explanatory theories have been set forth. Literature on this matter is somewhat contradictory, probably because of the complexity of drought resistance which may be effected in numerous and diverse ways.

Today, plant breeders are interested in varietal selections which, for the

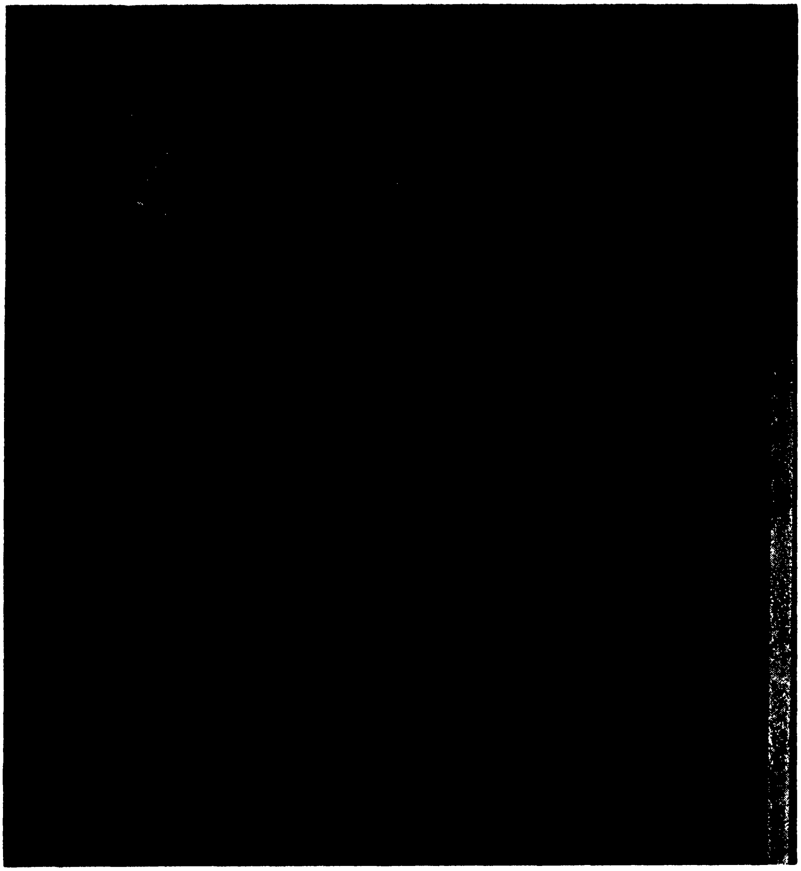

FIG. 5. Plants of *Bromus inermis* as they appeared at 6 months of age. Left to right, selections L-7, L-5, H-1, and H-6. Roots do not appear in normal lateral spread because of compacting for photographing.

most part, display no readily observed characteristics that would enable classification into categorical drought resistance groups. As a result of this fact, many methods have been devised to test these strains, many of which are based upon a single factor contributing to drought resistance, while others take in to account several of these factors.

There are three major factors involved in drought resistance, namely: (A) anatomical structure of the plant, (B) physico-chemical properties of the protoplasm, and (C) root development, especially in relation to top growth. The first two are concerned primarily with enabling the plant to retain moisture against the drying affects of the atmosphere, whereas the latter is concerned with means of attaining the moisture. Many plants effect drought resistance entirely in the former ways, others mainly in the latter. The present study deals entirely with root development, though it is appreciated that the former two factors may be fully as important and that, in some species, the root characteristics are of no value whatsoever as a measure of drought resistance.

In this study with eight *Bromus inermis* strains it was believed that selections H-1 and H-6 displayed root characteristics desirable for drought resistance in comparison to selections

L-5 and L-7 which exhibited root development less effective for resisting drought.

It is concluded that total axial length of roots (length of root axis excluding branches) is one of the best single measures for evaluating the root system for drought resistance since it takes into consideration all of the main roots produced by the individual plant. In most cases, length of "small" roots alone was found to be as valuable an index to drought resistence as was length of "small" roots plus length of "large" roots. This may be accounted for by the great variability in number of "large" roots and by their relative shortness. Neither of these measurements, alone, however, is a basis for complete evaluation of the root system without knowledge of depth, density, lateral spread, and amount of branching. Depth is especially important in the areas of winter precipitation where surface soil during the growing season may become dry to depths of several feet. In addition to these measurements, average root depth and root weight may be important bases for evaluating the root system for drought resistance.

The top and root weights and their ratios yield valuable information in comparing drought-resistant and non-resistant selections although, in most cases, the differences found in this study were of insufficient magnitude to be statistically significant. Weight of roots is not considered as valuable as are linear measurements because it ignores the extent and diameter or functioning surface of the individual roots.

It seems plausible to assume that differences in development would have been still more contrasting had dry soil and adverse weather accompanied the study. This developmental difference might have been especially great during the late summer period since, during July and August, all measurements and weights including top to root ratios decidedly favored the more drought-resistant selections. This would enable these plants to grow despite drought and, thus, to increase still further the advantage gained by deeper and more extensive root systems over non-resistent selections, which would have been forced into dormancy.

This study indicated that if selections show ability to survive controlled drought tests in the seedling stage and if they also produce deep, dense, and extensive root systems under field conditions they, in all probability, are possessed with a high degree of drought resistance.

SUMMARY

During the months from March to October, 1941, at Logan, Utah, an investigation was conducted on root and top growth of *Bromus inermis* selections exhibiting differences in ability to withstand controlled artificial drought tests in the seedling stage. Eight selections were grown under favorable field conditions in randomized and replicated rows. Their root systems were isolated for observation at six stages of development during their first season of growth.

Two types of roots were found; one larger in diameter and lighter colored, and the other smaller, darker, and more extensively branched. The latter composed the major portion of the root system. Measurements of "large" roots were found to be a less reliable index to drought resistance than those of "small" roots.

On the basis of root extent and ability to withstand controlled drought, selections were chosen as representative of drought-resistant strains for comparison to others chosen as representative of less resistant strains.

No significant differences were found in lateral spread of roots between the resistant and non-resistant groups. The resistant strains were consistently high in numbers of both "large" and "small" roots, and, in most cases, possessed significantly greater average root depths than less resistant strains during the entire season.

It was concluded that total axial root length was one of the best single measurements for evaluating root systems of *Bromus inermis* but that it was incomplete unless supplemented by other measurements. Resistant strains yielded significantly greater total axial lengths than non-resistant strains at each date of excavation without exception.

In general, the resistant selections made a more vigorous herbage growth throughout the season than did those less drought resistant.

The top and root weights including their ratios were found to favor the more drought-resistant selections but differences were not of sufficient magnitude, in most cases, to be used as dependable indices. The resistant selections were found to possess greater root weights in proportion to top weights than non-resistant.

The methods now employed for testing selections for drought resistance, without exception, fail to give adequate attention to the rôle of the root system, which though unimportant in some species, is of fundamental importance in determining drought resistance among many plants.

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SIZE OF BREEDING POPULATIONS IN RELATION TO EGG-LAYING AND REPRODUCTIVE SUCCESS IN THE EASTERN RED-WING (*AGELAIUS P. PHOENICEUS*)[1]

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The role of exteroceptive factors in relation to mating and reproductive success has long been a matter of interest. Much attention has been given to the biological significance of courtship patterns of behavior in many animals and particularly in birds (Whitman, '19; Matthews, '39 and citations). The apparently sound conclusion has been reached that such behavior has survival value (Howard, '29; Marshall, '36, '42). Studies of this nature received a new impetus from the growing recognition of the importance of animal aggregations in many phases of biology (Allee, '31; '38).

A few years ago Stresemann ('28, p. 407) found that small tern colonies produced a smaller percentage of offspring than did larger colonies and suggested that the larger colonies were more efficient in driving away marauding gulls. More recently, Darling ('38) has focused attention upon the functional significance of the numbers present in breeding groups of birds by his observations upon herring gulls (*Larus a. argentatus*) and lesser black-backed gulls (*Larus fuscus affinis*). The findings and ideas of Darling will be reviewed briefly since they furnished the stimulus for and general orientation of the present study.

Darling recognized three effects of colony size upon breeding activities of these gulls. The larger colonies showed (a) an earlier beginning of laying, (b) a greater synchronization of breeding and (c) a higher reproductive success.

If we focus upon his most convincing data, viz., those for herring gulls in 1936, the findings were as follows: the largest colony of 84–90 gulls began laying on May 7 and finished on May 23, 17 days inclusive; 40 functional nests held 84 eggs which yielded 35 fledglings, a reproductive success of 42 per cent.

The second colony of 30–34 gulls started laying on May 12 and finished on June 3, 23 days inclusive; 12 functional nests held 26 eggs from which 8 (31 per cent) reached fledgling age.

The third colony of 20 birds began laying on May 18 and finished on June 12, 26 days inclusive; the 7 nests with eggs held 16 eggs from which 3 chicks (19 per cent) were fledged.

The fourth colony of 4 gulls did not build nests until after May 26 and laid no eggs.

Darling interpreted these results, together with a review of pertinent literature, to mean in general terms and in part as follows (p. 76): "I suggest that in birds social at the breeding season, the importance of synchronization ex-

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[1] The present paper is based on a doctor's dissertation (see bibliography) which has been entirely rewritten for publication. The original manuscript is on file in the libraries of the University of Chicago and may be consulted for additional details. I wish to express my gratitude to Dr. W. C. Allee who originally suggested this problem and under whose direction it has been conducted. I am especially grateful to him for his aid in revising the manuscript for publication after my induction into military service. I am also indebted to Dr. Thomas Park for his immediate supervision of the work during the summer of 1939. Thanks are extended to Dr. Charles E. Olmsted and to Mr. Karl P. Schmidt for identifications; to Dr. Victor H. Dropkin for photographic assistance and for aid in the field; to Mr. Kenji Toda for drawing the graphs; to Mr. Asher J. Finkel for aid with statistical analyses; and to Mr. Rudyerd Boulton and Mrs. Margaret M. Nice for helpful advice and criticism. Much of the work was done while the writer held a Robert Ridgway Memorial Fellowship at the University of Chicago.

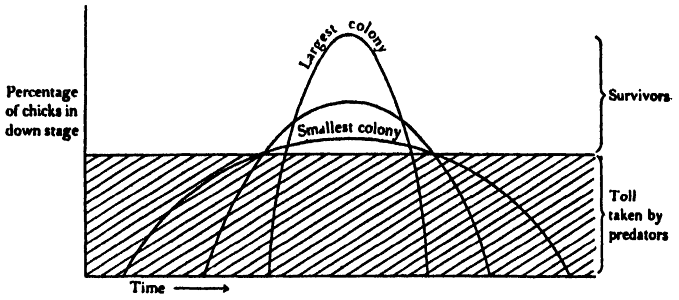


FIG. 1. A diagram which illustrates "how the survival rate is influenced by the 'spread' of time in which the eggs of a colony of herring gulls are laid."

tends to the ecological field of survival rate. That state is brought about by the same means of courtship display which synchronizes pairs of birds, but, in addition, the numbers of the flock are a potent factor because of the quantitative and cumulative value of their presence, general activity and courtship display. My observations show that as well as better synchronization of the breeding cycle, the onset of egg-laying is slightly earlier in the larger flocks. I do not suggest any particular survival value to rest in this phenomenon. . . ." Darling summarized his idea of the relation between synchrony of breeding and reproductive success in the diagram which is given here as figure 1.

These interesting observations and interpretations suggest two further types of investigation: In the first place, it is important to study intensively the relation between size of nesting colonies and onset of breeding, synchrony of breeding, and reproductive success in gulls and more or less closely related species in order to test for the generality of these phenomena among such birds in a variety of breeding locations. Second, tests are also needed concerning the universality of such relations among colonially nesting birds of many taxonomic ranks and ecological habitats. The present study is a contribution toward this second objective.

THE EASTERN RED-WING AS RESEARCH MATERIAL

The eastern red-wing was chosen for the present study for a number of reasons. As Mayr says ('41): "Red-wings can be considered, with certain reservations, to be colonial birds. We find that even in large marshes the nests are invariably clustered in a semi-colonial fashion." This species is found abundantly in the vicinity of Chicago as are the habitats in which it breeds. Many typical cat-tail (*Typha*) marshes exist which vary in size from a square rod or so to many acres in extent. Other marshy vegetation in which red-wings breed is also found nearby. A further reason for working with red-winged blackbirds came from the fact that many of its basic ecological relations are well known from the studies of Allen ('14), Mayr ('41) and others. I have relied much on the findings of these students, particularly upon Allen's work which was done at approximately the same latitude as Chicago. His observations have been verified at all points which were mutually touched at least as much as might reasonably be expected considering the differences in locality and the probable seasonal variations. Allen's paper should be read, or reread, to get a background of general life history and ecological relations; an effort will be made to avoid restating any such matters in the present discussion.

The advantage furnished by red-wings and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) for such studies has been appreciated by others. Since the present study was begun, Mayr ('41) has published data showing that in contrast to Darling's findings with gulls, egg laying may start earlier in smaller colonies of red-wings than in larger ones. And Fautin ('41a) has evidence that the yellow-headed blackbird had greater nesting success in the larger of two colonies studied.

Throughout, the number of males in a given habitat was determined by counting individuals that had established territory. The number of females in the larger colonies was estimated by counting nests.

In beginning the study, the summer of 1939 was spent in a reconnaissance of many available cat-tail and other breeding localities in the vicinity of Chicago. During 1940 a preliminary investigation of the breeding localities was conducted over a three-month period which extended from the middle of March until the middle of June in localities which were selected for intensive study. Because of retarded red-wing breeding in this year, a complete analysis of their reproduction in the various marshes was not obtained. In 1941, however, an investigation of the 1940 as well as a few new study localities was begun during March and continued through August. In this year the writer took up residence near the localities which were to be investigated, and made intensive observations from the middle of April until the end of July. An automobile was used to travel between certain marshes which were far apart.

Description of Study Localities

The reproduction of red-wings was followed in detail in 25 localities in the south-western part of Cook County, Illinois. Table I shows the number of individuals which bred in each of these study localities during 1940 and 1941.

The largest of these marshes (Locality 22c) consisted of approximately 5 acres and was located immediately north of Illinois highway 7 on the Orland Wildlife Refuge in the vicinity of Orland Park, Cook County, Illinois. A dense growth of cat-tails (*Typha latifolia* and *Typha angustifolia*) comprised the principal type of vegetation (pl. Ia). An irregular fringe of bulrushes (*Scirpus fluviatilis*) and bur reeds (*Sparganium eurycarpum*) grew about the periphery of the cat-tails. There were relatively few openings in the marsh, although a narrow channel of open water extended along the eastern margin. Drainage through the marsh was in a south-easterly direction, and thence by means of an intermittent creek into McGinnes Slough, an extensive, shallow body of water in the vicinity. Other more extensive cat-tail marshes occur relatively nearby which are more directly associated with the McGinnes Slough complex. The birds in Locality 22c will be referred to as group A or the colony at Orland.

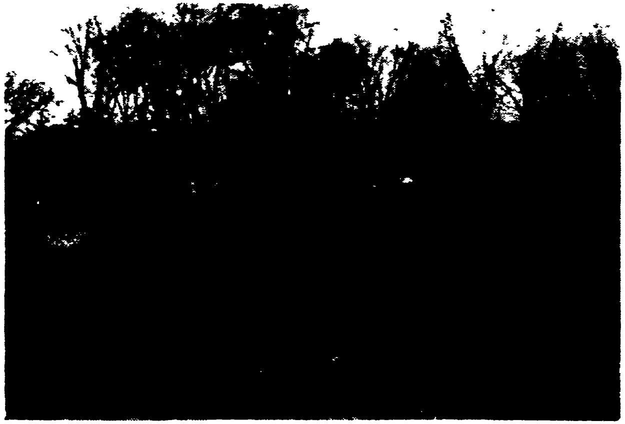
The 24 smaller localities were located in three general areas. Eighteen were on the extensive property of the Fifth Forest Preserve District of Cook County near Sag Bridge and Orland Park; the remainder were on private property. Only 19 of the 24 localities were studied in 1940. These localities and their inhabitants will subsequently be known as the marshes or red-wings of group B. Again the populations are summarized in table I both in general and in detail.

The Tinley Creek Woods area is located on fairly level ground near the eastern border of the Valparaiso moraine. Eight adjacent ponds and marshes, which were well-isolated from any other red-wing breeding localities, were present in this area. Cat-tails comprised the vegetation of two of these marshes. The nesting cover in one pond consisted of bulrushes. A summer-dry pond supported marginal vegetation of cat-tails and bur reeds on opposite shores. One locality was a marshy depression in

PLATE I

a. Locality 22c.

b. Locality 319b.



c. Locality 3a.

Photos by Dr. Victor H. Dropkin.

TABLE I. *Adult populations of study localities in groups A and B during the breeding seasons of 1940 and 1941*

Locality	Cover	1940		Completed nests	1941		Completed nests
		♂♂	♀♀		♂♂	♀♀	
Group A							
Orland Wildlife Refuge							
22c	*Typha*	??	122	128	40+	about 110	167
Group B							
Tinley Creek Woods area							
29bs	*Typha* and *Sparganium*	1–2	2	2	1	2	4
29bt	*Sparganium*	0	0	0	1	1	1
29bu	*Cephalanthus*	1–2	?	0	1	1	2
29bv	*Typha*	1	1	1	1*	1*	2
29bw	*Sparganium*	1	1	1	2	4	6
29bx	*Cephalanthus*	2	3	3	1	2	4
29by	*Typha*	4	8	8	3	11	24
29bz	*Scirpus*	1	2	2	1	2	3
Bell Road area							
28a	*Typha*	1–2	?	0	0	0	0
28b	*Typha* and *Sparganium*	2–3	6–7	9	1	2	3
528b	*Sparganium*	1	1	2	0	0	0
528c	*Typha*	3–4	10–11	14	1	1	1
320a	*Typha*	—	—	—	1	2	3
Red Gate Woods area							
30a	*Scirpus*	1	3	3	1	2	3
30b	*Typha*	4	11	11	5	15–17	24
30c	*Typha*	0	0	0	1	2	2
320b	*Solanum*	—	—	—	1	1	1
528a	*Cephalanthus*	1	2	3	1	1	2
428a	*Typha*	2–3	4	6	2	6	8
324a	*Typha*	—	—	—	5	19	25
321a	*Typha*	—	—	—	1	1	3
Mount Forest Island area							
319b	*Typha*	—	—	—	8–12	34	57
513a	*Typha*	2	6	7	1	3	6
3a	*Typha*	1	3	3	3	3	5
Total of study localities in B		29–35	63–65	75	42–46	115–117	189

* This pair of individuals is identical with the pair of Locality 29bt. The male maintained a territory which comprised both of these adjacent ponds; and the female interspersed an unsuccessful nesting attempt in Locality 29bt between two nestings, both of which were also unsuccessful, in Locality 29bv.

which there was a fair growth of *Sparganium*, and one was a permanent pond which was fringed with bur reeds. The remaining two localities were brushy ponds in which there was a vegetation of buttonbushes (*Cephalanthus occidentalis*).

Five marshes and ponds were located in fairly close proximity on private property in the Bell Road area near Sag Bridge, Illinois. There were no other nesting red-wings within approximately 350 yards. These habitats were shallow depressions in a cattle pasture, and were situated on glacial till of the Valparaiso moraine. Cat-tails comprised the principal type of vegetation in four of these marshes; a clump of bur reeds also contributed to the nesting cover in one locality and a restricted growth of these reeds in a pond was the fifth nesting habitat in this area. Cattle trampled and grazed upon the aquatic vegetation of these marshes during the dry summer of 1940. As a consequence, there was, throughout the breeding season of 1941, very little cover provided by standing vegetation of the preceding year. It was not until the middle of May that the growing vegetation of 1941 was sufficiently dense to provide adequate cover for any nests. And since the height of early reproduction in the study area had already begun to decline at this time, the total red-wing population here was much lower in 1941 than in the preceding year.

Eight marshes and ponds were situated in the Red Gate Woods area near the western edge of Mount Forest Island in a region of low red-wing density. Mount Forest Island is a knob and kettle remnant of an insular area during an earlier epoch in the history of recession of Lake Michigan. The density of population of red-wings becomes progressively higher in an easterly direction. Cat-tails grew in five of these marshes. In one pond the nesting cover consisted of bulrushes. A thicket of buttonbushes was present in another pond and the eighth breeding habitat was a moist depression in which the vegetation consisted of bittersweet shrubs (*Solanum dulcamara*). During 1940 only five of these localities were studied, in one of which no red-wing reproduction occurred. In 1941 all eight of the localities were populated with a total of 17 males and 48 females.

One of the three remaining habitats was located in an easterly direction in the central part of Mount Forest Island. This marsh, known as Locality 319b, was unstudied in 1940. It was an open-water pond of intermediate size which supported a fairly dense growth of cat-tails along its margins (pl. Ib). Its 1941 population of 8–12 males and 34 females was the largest of these smaller breeding aggregations of red-wings. The second locality, a cat-tail depression, was located farther east in the vicinity of a larger, unstudied pond fringed with the same type of vegetation. The third locality (pl. Ic) was a small, mature *Typha* marsh located on private property near the eastern edge of Mount Forest Island.

Population Size

Without data for a much longer period, it is impossible to estimate the numbers which these habitats can carry or to discuss the recorded populations in relation to minimal, optimal or maximal breeding populations. The weather for 1940 and 1941 differed greatly. The former year was much colder during April and early May and nesting was accordingly retarded. Yet the number of red-wings present was of the same order of magnitude for the two years. Thus, as shown in table I, 122 females built 128 early nests at Orland in 1940 as compared with about 110 females which constructed 131 nests in brood I for 1941.

Of the B marshes which were studied in both years, where conditions were comparable the total populations were 68–71 adults for 1940 (50 nests) as compared with 79–81 for 1941 (84 nests). In getting these figures the marshes in the Bell Road area were omitted because of changed physical conditions. If they are included, the figures become 92–100 for 1940 (75 nests) against 84–86 for 1941 (87 nests). This indicates that there was no great difference in size of breeding populations in these localities for these two years.

Outline of Study

The present investigation is a comparative study of the beginning of breeding, the temporal spread of egg-laying, and reproductive success in (1) an extensive breeding colony of red-wings (group A) and (2) an equivalent number of individuals breeding in limited groups throughout the area (group B).

Table I shows that in 1941 there were fewer than ten adults per locality in 18 and fewer than five adults in 15 of the 22 inhabited marshes of group B. In

1940, only 4 of the 17 occupied breeding habitats contained as many as 10 adults each. Groups A and B thus constitute two numerically equivalent populations which differ (1) in numbers of red-wings breeding in the given habitats, (2) in size of habitat which is suitable for red-wing nesting, (3) in duration of suitability and (4) in type of nesting cover. The data which are discussed in the present paper have been analyzed, upon a comparative basis, primarily with respect to variation in size of breeding colony between these two groups of individuals. The habitat differences between the two are not entirely neglected. Further work is needed before the differences in physical or plant characteristics of the habitats can be properly evaluated.

Methods

The procedure used throughout the study was to tag nests. This was usually done during an early or intermediate stage of nest construction. In 1940 numbered adhesive-tape labels were used. During 1941, tags were nearly all made of galvanized sheet steel, on which a number had been stamped; a few adhesive labels were also used. The tag was attached in an inconspicuous position on the supporting vegetation of the nest. In 1941 the nests were usually visited no less frequently than on alternate days, and pertinent data were recorded in field notes. These were transferred to more permanent records at the conclusion of the study.

Insufficiency of time in relation to an extensive analysis of numerous red-wing breeding populations prohibited any banding studies in the present investigation. The need for this added refinement was recognized from the beginning. Every allocation of a nest with respect to its proper brood is therefore based entirely upon the spatial and temporal distribution of the various nests in question. As Allen ('14, p. 95) states, a nest of a double-brooded female is constructed in the immediate vicinity, and frequently within a distance of ten feet, of an original nest; this also applies to renestings which follow completely unsuccessful original nestings. Allen's method of correlation between an original nest, a renest following disturbance or destruction of the first, or a second nest in the case of double-brooded females is considered to be a fairly adequate basis upon which to establish these relationships. More precisely, a new nest was recorded as a renest if it was first discovered in the field shortly after the destruction of an earlier nest which had been built in the immediate vicinity. Similarly a new nest was recorded as a nest of brood II if it was built nearby immediately following the departure of young or while young were in an advanced stage of development in the original nest.

In this paper total figures for time relations of egg-laying and for reproductive success will be stressed. The more obvious indications will also be presented for broods I and II in groups A and B. Little attempt is made here to break down data of any particular brood into original nestings and renestings. The analyses of this sort which were tried in a preliminary fashion in no way modify the general results.

The area of every study locality was found by tracing outline drawings of commercially prepared aerial photographs of these marshes and ponds by means of a polar planimeter.[2] The extent of margin (edge) in these localities was obtained from these aerial photographs by running a map measuring wheel around an outline drawing of the periphery of every locality and around the margins of its openings. Such figures of edge are necessarily approximations since the boundaries of openings in a marsh are frequently difficult to distinguish in an aerial photograph and since highly precise readings of linear distances cannot be obtained with a map measuring wheel of the sort which was used in this work. In addition, the boundaries of many of the margins varied as the season progressed.

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[2] The scale of these photographs was approximately 1 inch per 144 feet for the marsh at Orland, and 1 inch per 262 feet for the other 24 marshes and ponds.

A knowledge of the date on which every egg was laid in 1941 has provided the basis for determining the beginning and the span of egg laying in the two major categories of individuals. Reproductive success has been based upon the number of nestlings which were fledged as juveniles, and was determined by following each nest until after the nestlings had left the nest, or until after mortality had occurred. Usually it was fairly easy to follow in a general way the history of each nest. For example, infertility of eggs was easily recognizable as such. Destruction of eggs or nestlings by predators was also distinguishable from death following desertion of eggs or trampling of nests by cattle. Table II represents an analysis of these factors of mortality in groups A and B during the breeding season of 1941. Of the various types of mortality, predation of eggs and nestlings contributed the highest percentages in both groups of individuals.

TABLE II. *Causes of mortality in groups A and B during the breeding season of 1941*

	A		B	
	No.	%	No.	%
Total number of eggs laid	563		577	
Egg loss				
1. Elemental				
a. Wind	4	1.8	5	2.1
2. Biotic				
a. Growth of vegetation	0	0	3	1.3
b. Predation	87	38.3	120	51.1
c. Death of adults	15	6.6	9	3.8
3. Physiological				
a. Infertility	19	8.4	18	7.7
b. Loss at hatching	12	5.3	9	3.8
c. Desertion	8	3.5	5	2.1
d. Egg-removal	0	0	3	1.3
Total eggs lost	145	63.9	172	73.2
Nestling mortality				
1. Elemental				
a. Drowning or exposure	8	3.5	0–1	.2
2. Biotic				
a. Predation	70–72	31.3	56–59	24.5
b. Trampling of nests by cattle	0	0	3	1.3
3. Physiological				
a. Mortality at hatching	2	.9	1	.4
b. Starvation	1	.4	1	.4
Total nestling mortality	81–83	36.1	61–65	26.8
Total mortality	226–228	100	233–237	100

In cases of predation it was usually difficult to determine the species of predator inasmuch as relatively few instances of this type of mortality were actually witnessed. Bluejay and crow feathers were found near nests in which eggs had been destroyed and a snake identified as *Elaphe v. vulpina* is known to have inhabited one marsh. Flocks of grackles and starlings roosted in certain of the marshes during early spring, but there is no evidence of their role as predators. Unidentified mammalian faecal pellets were found in one nest.

ESTABLISHMENT OF TERRITORIES AND NEST BUILDING

The establishment of territories at Orland in 1941 began during the middle or latter part of March and continued into early April. Territories were established in certain of the marshes and ponds of group B as early as at Orland. However, this process continued further into April in a few of the restricted localities of this group than at Orland. Possibly this is related to an inhabitation of certain of these localities by young males. At least males with duller brownish feather tips both on body and wing coverts were seen to take up territories in these smaller marshes during April. Such individuals supposedly migrate later in the spring than do older resident adult males (Allen, '14, p. 86, p. 95). The arrival of resident female individuals began during early April. Sexual chasing and other aspects of courting were conspicuous during the middle of April at which time nest building was begun.

In early spring as many as 7 days may pass after completion of a nest before eggs are laid; subsequently the interval is shortened to one or two days.

In part, the developing sequence is broken by introducing the following details at this point. However, they have an important bearing on the date of onset of given reproductive activities in the large breeding population at Orland as contrasted with the smaller groups of red-wings and should be presented here. In 1940 red-wing breeding was held up by a cold and retarded spring, and no nests were found in any locality on May 4. On May 6 at Orland, there was one completed nest without eggs. Eggs were laid in this nest on May 14, 15, 16 and 17, one egg each day as is usual in this species. The first nestlings were seen on May 29 when there were three young and one egg in the nest. Hatching probably occurred on May 28.

In comparison, among the marshes of group B, the first nest in 1940 was found on May 12 in marsh 3a. It contained one egg and may have been completed as early as the first nest at Orland. Eggs were laid on May 12, 13 and 14 and all three eggs hatched probably on May 25; three young were present on May 31. This set of eggs and nestlings preceded the earliest ones in the large colony. Locality 3a contained 4 adults.

In 1941 nests were frequently visited daily during early spring, and for these early nests and under these circumstances, the interval between observations was never greater than two days. The following sequences of first observations were recorded:

At Orland, the first nest was found on April 16 (it may have been begun on the preceding day); first egg, April 21; first nestling, May 4 (probably hatched on May 3); first fledgling, May 14 or 15.

Among the B marshes, the first nest was in Locality 3a and was found on April 17. It may have been begun on April 16. The first egg was laid on April 23; first nestlings, May 6 (3 young plus 1 egg) or May 7 (4 young). Two young had left the nest on May 17; they could have left on May 16. There was an adult population of 6 birds in this nesting population.

Thus in 1940, egg laying and development up to the fledgling stage was slightly ahead in one of the smaller breeding colonies; in 1941, the larger colony was 1 or 2 days ahead. Both differences were slight and probably lack significance. It is interesting to note that in 1941, the first female to deposit eggs in the B marshes, laid her clutch of eggs on April 23, 24, 25 and 26 and no other female began laying until April 30. Hence, this one bird aside, the onset of general egg laying started considerably later in the scattered marshes than it did in the large colony at Orland.

EGG-LAYING

The present data concerning egg-laying are based upon eggs which were deposited in nests in the study localities during 1941. The data for 1940 are excluded because they were not collected frequently enough and because field-work had to be discontinued before the breeding season was concluded.

When the total time span for ovulation in groups A and B is considered (figure 2), it is seen that the least synchronous span of ovulation was that of the breeding colony of greatest magnitude. Egg-laying, in group A, began two days earlier in April and was protracted further into July than in any or all of the restricted localities in group B. As figure 2 shows, egg-laying commenced at Orland (solid line) on April 21 and continued over an 83 day period which extended until July 12 with a series of four consistently diminishing peaks. The earliest of these peaks consisted of 38 eggs and was attained on May 9. A second peak on May 22 followed a general decline in egg production which culminated on May 20. This second peak represents renests of brood I that followed completely unsuccessful original attempts as well as a few original nestings of brood I and early original nests of

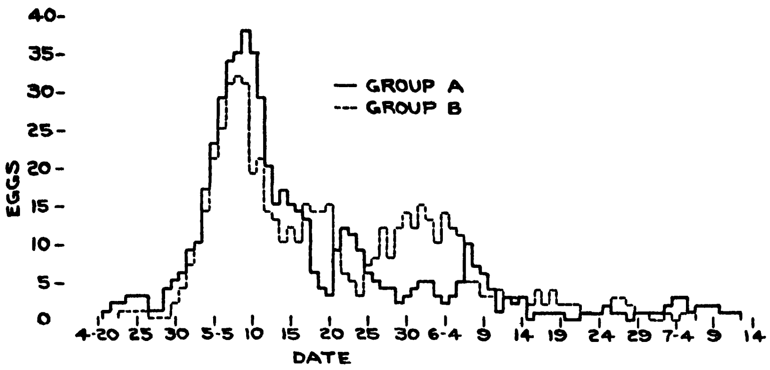

FIG. 2. Total span of egg-laying in groups A and B during the breeding season of 1941.

brood II.[3] A third peak on June 7 is at the height of the initial nests of brood II. A slight rise in egg-laying early in July is more difficult to explain; it was originally believed to be a result of triple-broodedness and may in fact represent this phenomenon.[4] In order to be conservative, these will be referred to as the July eggs or brood.

In group B (broken line) egg-laying began on April 23 and extended over a 75 day period which ended on July 6 (figure 2). There were three general peaks of egg-laying. The highest of these peaks, which represents eggs of original nestings of brood I, comprised 31 eggs and was reached on May 8. A lesser peak, only partially separated from the preceding peak, extended from May 17 to May 20; it consisted primarily of renestings of brood I which followed completely unsuccessful original nestings. A third broad peak during the end of May and early part of June represents renestings of brood I and original nestings of brood II. There was no evidence of a rise in egg-laying during July.

The earliest onset of reproduction in the largest colony in 1941 is in accordance with Darling's findings in gulls. The prolongation of egg-laying into the fag end of the breeding season in group A appears superficially to indicate a lesser synchrony of egg-laying in the largest colony and this is in contrast to Darling's observations for gulls. However, as has already been mentioned, this continuation of reproduction is correlated with other conditions which made interpretation difficult. In order to obtain a better understanding of the facts, it may be helpful to break down the observations in terms of field estimates concerning original nestings and renestings of the different broods in the two major categories of individuals.[5]

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[3] Double-broodedness in *A. phoeniceus* is well known and has been discussed at length by Allen ('14). It is possible that a few of the nests which were assigned in the field to brood II in reality belong to brood I. They may have been constructed by immature females which are supposed to migrate and breed later than older resident adult females (Allen, '14, p. 86).

[4] Triple-broodedness is well known for this species in the southern part of its breeding range; it has been recorded near Ypsilanti, Michigan by Peet ('08, p. 165) who states that "two or three broods are usually raised." The presence of a third brood at Orland in 1941 is not conclusively indicated by available data. The nests which were built during July may represent (a) original nests of brood I for resident immature females; (b) renests of late nesting females in brood I; (c) original nests of brood II of females which had previously nested elsewhere in the area and then shifted into the marsh at Orland following the drying up of their former habitats. Intensive banding operations are needed to test critically this matter of triple-broodedness in red-wings in northern Illinois. The nests in this July brood were not closely related to any earlier nests. In general they were distributed about the few remaining areas of open water which extended along the eastern margin of Locality 22c.

The adult population of about 110 females which constructed 131 nests of brood I at Orland deposited 455 eggs over a 45 day period which extended from April 21 until June 4 (figure 3). The peak was attained on May 9 when 38 eggs, 8.4 per cent of the total number of eggs of brood I, were laid. During a 7 day peak which extended from May 5 to May 11 a total of 223 eggs, 49.0 per cent of the eggs of nests of this brood, was deposited. On one day (May 30) of this 45 day span there were no eggs of brood I deposited in this locality. There is thus a period of only 39 days during which there was a daily deposition of one or more eggs allocated to this brood in this marsh.

In group B, the total number of 115–117 females which constructed 155 nests of brood I deposited 484 eggs over a 75 day period extending from April 23 to July 6 (figure 3). The peak was attained on May 8 on which day 31 eggs, 6.4 per cent of the total number of eggs of this brood, were laid. As at Orland, the seven most productive days in group B extended from May 5 to May 11. During this 7 day period, 176 eggs, or 36.4 per cent of the total number for brood I, were laid. There was a period of 43 days, extending from April 30 to June 11, during which a minimum of one egg was deposited every day in these localities. One early nesting female and one female which laid during July are primarily responsible for extending this period of egg-laying to 75 days. The later nests allocated to this brood were judged to be renestings following the destruction of the original set of eggs or nestlings.

Graph 3 indicates that the highest one-day peak of egg-laying in brood I was slightly higher in A than in B. Similarly, there was a 12.6 per cent higher 7 day peak of egg-laying in A than in B. The duration of egg deposition assigned to brood I was 30 days longer in B than in A. This is a rather convincing indication for this brood of a higher synchronization of egg-laying in the extensive colony of red-wings.

A somewhat different relationship exists between the spans of oviposition of brood II in the two groups of red-wings. In group A, 25 females, which constituted an incidence of double-broodedness of 22.7 per cent, deposited a total of 91 eggs in 30 nests allocated to brood II. The span of these ovulations (figure 4) extended over a 50 day period with a peak of 10 eggs (11.0 per

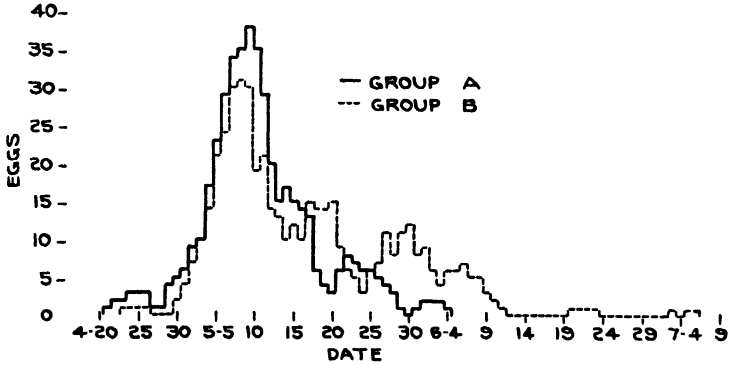

FIG. 3. Span of egg-laying of brood I in groups A and B during the breeding season of 1941.

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[5] There was very little doubt in assigning the majority of nests of this study to their proper broods. However, as has been mentioned earlier, an intensive banding investigation is the only critical method of correlating red-wing nests with their respective females.

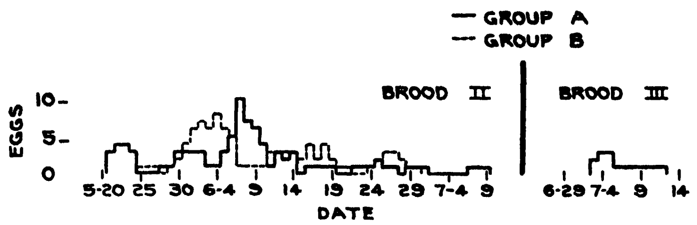

FIG. 4. Span of egg-laying of brood II and the July brood (III) in groups A and B during the breeding season of 1941.

cent) deposited on June 7. In B, 27 females, which constituted an incidence of double-broodedness of 23.3 per cent, deposited a total of 93 eggs in 34 nests of brood II. In this category, the span (figure 4) extends over a 37 day period with a peak of 8 eggs (8.6 per cent) on June 4. With respect to brood II, the peak of ovulation is again higher in A than in B, although there is a longer span of egg-laying at Orland than in B. This may well be an expression of a prolongation of satisfactory breeding conditions in the large marsh at Orland.

There were six females (see footnote 4) which may represent an incidence of triple-broodedness of 5.5 per cent at Orland during 1941. These six females deposited 17 eggs over a known 10 day period which extended from July 3 to July 12 (figure 4). As has been stated earlier, there was no evidence of a rise in egg-laying during July in group B.

By way of summary the following facts may be stated for the breeding season of 1941. (1) The least synchronous total span of reproduction was that of the breeding colony of greatest magnitude. (2) Egg-laying began earlier and there was a higher synchronization of the span of egg-laying of brood I in A than in B. This is in line with Darling's observations for gulls. (3) Again the peak of egg-laying of brood II was higher in A than in B. In this case there was a longer span of egg-laying in A. There were similar percentages of double-broodedness in A and B. (4) There was a slight rise in egg production during July in the large breeding marsh.

REPRODUCTIVE SUCCESS

A third suggestion of Darling's ('38) and one on which he placed much emphasis concerns the ecological survival value or relative breeding success of larger colonies of breeding birds. In the present discussion reproductive success is calculated in terms of the percentage of individuals which were fledged as juveniles in relation to the total number of eggs deposited. The figures of egg and nestling mortality similarly represent percentages of the total number of eggs which were deposited. No attempt has been made here to study the death rate among fledglings.

There is no real difference between the total percentages of reproductive success in the two categories of red-wings. In 1941, at Orland, there was a total of 563 eggs (5.12 per ♀) deposited throughout the breeding season (table III). Of this number, there was a loss of 145 eggs (25.7 per cent) and of 81–83 nestlings (14.6 per cent). These figures indicate

TABLE III. *Total figures of mortality and reproductive success in groups A and B during the breeding season of 1941*

	Females	Eggs	Egg mortality	Nestling mortality	Reproductive success
Group A	about 110	563	145 25.7%	81–83 14.6 ±.18%*	335–337 59.7 ±.18%
Group B	115–117	577	172 29.8%	61–65 10.9 ±.35%	340–344 59.3 ±.35%

* Percentage represents a mean figure wherever there is an uncertainty about the mortality or success of any nestlings; ± designates greatest error which may be added or subtracted in order to obtain limits of this discrepancy.

a total mortality of 40.3 per cent. Conversely, 335–337 individuals which were fledged as juveniles result in a total reproductive success of 59.7 per cent. Inasmuch as there was no July brood in B, it may be worthwhile to omit such eggs from consideration at Orland. Of 546 eggs deposited earlier, there was a loss of 137 eggs (25.1 per cent) and of 78–80 nestlings (14.5 per cent). This indicates a success of 60.4 per cent (table IV).

TABLE IV. *Mortality and reproductive success of broods I and II in group A during the breeding season of 1941*

	Females	Eggs	Egg mortality	Nestling mortality	Reproductive success
Group A	about 110	546	137 25.1%	78–80 14.5±.18%	329–331 60.4±.18%

In group B a total number of 577 eggs (4.97 per ♀) was laid in broods I and II during the breeding season of 1941 (table III). In this group there was a mortality of 172 eggs (29.8 per cent) and 61–65 nestlings (10.9 per cent). Summing the percentages of these two gives a total loss of 40.7 per cent. A total number of 340–344 individuals which were fledged successfully indicate a reproductive success of 59.3 per cent.

These results were analyzed statistically. The value of P was obtained from formula 19.4 given by Yule and Kendall ('40, p. 360) for the standard error of the difference between two proportions. A P-value of .05 is approximately equal to 2x the standard error of such a difference and is here regarded as the upper limit of statistical significance.

There is no real difference between the respective percentages of total reproductive success in the two categories of individuals. A high value of 0.89 which was obtained for P is an expression of the statistical insignificance of this difference. The incidence of egg mortality in B is 4.1 per cent higher than in A. Conversely, however, there is a slightly higher nestling mortality of 3.7 per cent in A than in B. If the data which pertain to the July eggs in A are omitted, the success of reproduction of the more highly comparable broods I and II is again insignificantly (1.1 per cent) higher in A than in B. P equals .69 in this analysis. These results give little or no support for a possible extension of Darling's hypothesis to reproductive success in the red-wing colonies studied.

An analysis of reproductive success in brood I of each category of individuals brings out further negative results with respect to Darling's hypothesis. At Orland, during 1941, a total number of 455 eggs was deposited in nests of brood I. Of this number, there was a mortality of 111 eggs (24.4 per cent) and 74–76 nestlings (16.5 per cent). The remaining 268–270 individuals which left nests as juveniles indicate a reproductive success of brood I of 59.1 per cent (table V). Incomplete results of 1940 indicate a mortality of 17 of 65 eggs, an egg mortality of 26.2 per cent, in nests of brood I. As a result of the early termination of study during 1940, there are no data concerning nestling mortality or reproductive success in this group.

TABLE V. *Mortality and reproductive success of broods I, II and III in groups A and B during the breeding season of 1941*

	Females	Eggs	Egg mortality	Nestling mortality	Reproductive success
Brood I					
A	about 110	455	111 24.4%	74–76 16.5±.2%	268–270 59.1±.2%
B	115–117	484	126 26.0%	48–52 10.3±.4%	306–310 63.6±.4%
Brood II					
A	25	91	26 28.6%	4 4.4%	61 67.0%
B	27	93	46 49.5%	13 14.0%	34 36.6%
July Brood					
A	6	17	8 47.1%	3 17.6%	6 25.3%

In B, corresponding data of 1941 indicate a total number of 484 eggs which were deposited in nests of brood I. Of these, there was a mortality of 126 eggs (26.0 per cent) and 48–52 nestlings

(10.3 per cent). A total of 306–310 individuals, or 63.6 per cent, were fledged successfully (table V). In 1940, partial results apply to a mortality of 26 of 115 eggs in nests of brood I. This gives an egg mortality of 22.6 per cent. Again, the data of this year are insufficient to establish any percentages of nestling mortality or total reproductive success in group B.

The success of reproduction of brood I during 1941 is thus 4.5 per cent higher in B than in A. This difference lacks statistical significance (P equals .16). The important fact is that there is no indication of greater survival value related to the greater synchrony of egg laying for this brood at Orland.

When the success of brood II in groups A and B is considered, a distinctly different type of relationship is seen to exist between the two sets of populations. Out of 91 eggs of this brood in the large colony at Orland there was a mortality of 26 eggs and 4 nestlings (table V). The 61 individuals which were fledged indicate a success of 67.0 per cent. In the scattered marshes of B, on the other hand, there was a mortality of 46 eggs and 13 nestlings out of a total of 93 eggs (table V). This leaves only 34 individuals, or 36.6 per cent, which were fledged successfully. A very high egg loss of 49.5 per cent contributes heavily to the high total mortality figure of this brood in group B. Statistically the reproductive success of brood II is significantly higher in A than in B (P equals .00004).

Only 17 eggs were deposited in the July brood at Orland and only 6 individuals (35.3 per cent) were fledged. The success of this brood is thus very low although the sample is too small to be of much significance. However, it is to be compared with the complete absence of this brood in group B.

A few other analyses of reproductive success in the various marshes of B during 1941 may be helpful in studying any possible correlation between the magnitude and relative success of a breeding colony. Locality 319b is an open-water pond of intermediate size which had a breeding population of 8–12 males and 34 females in 1941 (see table I). It is the largest of the 24 breeding colonies in B. A total of 178 eggs were deposited in 57 nests in this locality in broods I and II. Of these, there was a loss of 61 eggs (34.3 per cent) and of 16 nestlings (9.0 per cent). This leaves 101 individuals, or 56.7 per cent, which were fledged successfully. In the 23 remaining breeding populations of B there was, of 399 eggs deposited, a mortality of 111 eggs (27.8 per cent) and 45–49 nestlings (11.8 per cent). A total of 239–243 individuals which left nests successfully indicate a reproductive success of 60.4 per cent. The difference of 3.7 per cent is statistically insignificant (P equals .41).

Similarly, a comparison of the figures of reproductive success of broods I and II may be made in relation to a further re-arrangement of the localities of B. In this instance one grouping consists of Localities 319b, 324a, 30b, and 29by, each of which was populated by an excess of 10 adults; the other consists of the remaining 20 localities in which there were fewer than 10 adults in each breeding population. Of 398 eggs deposited in the four larger populations, there was a mortality of 122 eggs (30.6 per cent) and 42–43 nestlings (10.7 per cent). The total of 233–234 individuals which were fledged indicates a fledgling success of 58.7 per cent. In the remaining 20 localities, there was, of 179 eggs deposited, a mortality of 50 eggs (27.9 per cent) and 19–22 nestlings (11.5 per cent). The remaining 107–110 individuals which were fledged give a reproductive success of 60.6 per cent. The difference of 1.9 per cent lacks statistical significance (P equals .66).

The analysis of reproductive success in group B may be pushed a step further by distributing the 24 study localities among three minor groupings as follows:

(1) Locality 319b, the afore-mentioned marsh of intermediate magnitude, (2) Localities 324a, 30b, and 29by, three localities of fair magnitude, and (3) the remaining 20 localities in which, individually, there were fewer than 10 red-wings per locality. There is an absence of any direct correlation of reproductive success with the magnitude of breeding population in these various marshes. The figures are 56.7 per cent, 60.2 per cent and 60.6 per cent respectively. No real difference exists among these three figures or between any of them and the percentage of individuals (59.7 per cent) which left nests successfully at Orland during 1941.

Upon the basis of the present discussion the following conclusions may be drawn. (1) A negligible difference exists between the respective percentages of total reproductive success in groups A and B. (2) The reproductive success of brood I is statistically similar in the category of smaller populations (B) and in the large population at Orland. (3) There is a significantly higher success of reproduction of brood II in A than in B. (4) The success of the July brood at Orland is very low. (5) No obvious correlation exists between reproductive success and the magnitude of breeding population in various minor groupings of the study localities of B.

Reproductive success may also be analyzed from a somewhat different aspect, viz., that of the number of juveniles fledged per adult in the breeding population. Such an analysis for 1941 corroborates the conclusions just given. In A, 3.05 juveniles were fledged per adult female and 2.17 per adult male and female. This amounts to 2.01 fledglings for each completed nest. The corresponding numbers fledged for the scattered B populations were 2.95, 2.14, and 1.81 respectively. The smaller success per nest in B amounted to 0.20. None of the differences between A and B is impressive. In general terms, approximately the same breeding population in the two categories under consideration produced approximately the same number of offspring. The females in the smaller marshes constructed 22 more nests and hence had a slightly smaller reproductive success per nest which, however, is of no statistical significance. This method of analyzing reproductive success indicates clearly that the bulk of juveniles fledged during the breeding season are of brood I with 2.45 per female in A and 2.66 in B. The paucity of juveniles of brood II (0.55 per adult female in A in comparison with 0.29 in B) results primarily from a restricted incidence of double-broodedness in the adults of the marshes of the present region. The contribution of the July brood at Orland to the total number of juveniles is even less and amounted to only 0.05 per adult female of the original breeding population. This is, however, to be compared with an absence of any juveniles of this brood in B.

OTHER ASPECTS OF REPRODUCTION

Certain other data which have been analyzed in the present study concern (1) fecundity and fertility in *A. phoeniceus*, and (2) the incidence of intra-brood parasitism of red-wings by the eastern cowbird (*Molothrus a. ater*).

In determining fecundity only completed clutches of eggs have been considered. In 1941, at Orland, there were 3.66 eggs per completed clutch as compared with 3.69 for B. The difference is insignificant. There are data for both 1940 and 1941 for nests which were assigned in the field to brood I. For A, the values were 3.68 and 3.74 respectively per completed clutch as compared with the almost identical fecundity of 3.73 and 3.75 for B. These figures indicate that over a period of two years there was essentially no difference in fecundity of brood I between groups A and B. The fecundity of brood II in A during 1941 equaled 3.48 eggs as against 3.42 for B. These figures, while comparable between the two groups, are consistently lower than those for brood I. A total of 17 eggs in 6 nests of the July brood at Orland suggests an even lower fecundity of 2.83 eggs per completed clutch in this brood.

There is identity between the total figures of fertility in groups A and B during 1941. The fertility of 437 eggs in A and 423 eggs in B was 95.7 per cent. 50 eggs of brood I at Orland that were carefully followed during 1940 gave a fertility of 96.0 per cent. In 1941 a larger sample of 344 fertile and 16 infertile eggs of brood I in this group result in a comparable figure of 95.6 per cent. During 1940 in B sampling of 89 eggs of brood I showed a fertility of 100 per cent. In the following year a sampling of 372 eggs in this brood gave a fertility of 96.2 per cent. In 1941, the fertility continued at the same level for brood II in A inasmuch as 98.5 percent of 65 eggs hatched. In B, there was a possibly significant decrease in fertility since 92.5 per cent of a sample of 47 eggs hatched. Fertility dropped to 81.8 per cent for the July brood at Orland upon the basis of a sample of only 11 eggs.

As a summary it may be stated that there is no difference between the total figures of fertility in groups A and B. The percentages of fertility of brood I are also similar in A and B. The fertility of brood II apparently dropped slightly in B, perhaps as a consequence of the smallness of sample. In A, the July brood fertility dropped markedly, although the sample is again too small to be of much significance.

A few interesting results appear in connection with an analysis of parasitism of red-wings by cowbirds. During 1940, in B, no cowbird eggs are known to have been deposited in nests of red-wings. In 1941, however, there were 9 cowbird eggs deposited in a similar number of red-wing nests in B, an incidence of almost 5 per cent of parasitized nests. There were 577 red-wing eggs deposited in the B nests; hence the percentage of parasitism per red-wing egg is 1.6 per cent. Of these 9 eggs, there was a mortality of 8 eggs and 0 nestlings. One individual which was fledged gave a reproductive success of *Molothrus ater* in nests of *Agelaius phoeniceus* of 11.1 per cent. There was, in this instance, no mortality of red-wing eggs or nestlings associated with the parasitism. Four red-wing eggs which were deposited in this nest were also successful.

In 1940, at Orland, two cowbird eggs, an incidence of parasitism of 0.6 per cent, were deposited in a red-wing nest in which no eggs of red-wings had as yet been laid. These eggs did not develop since desertion of this nest followed without any deposition of red-wing eggs. The success of cowbird reproduction in this locality in 1940 is thus 0 per cent. During 1941, no cowbird eggs were deposited in A. This is in comparison with 563 eggs of red-wings which were deposited in nests of this locality. The possibility is suggested by these data that there may be an aggregate effect of numbers which retards or even prohibits the deposition of cowbird eggs in red-wing populations of high density. In view of the restricted incidence of cowbird parasitism and its apparent negligible effect upon red-wing mortality, it would appear that this factor is of relatively little importance in a consideration of the success of red-wing reproduction.

Discussion

It is well to refer to Darling ('38) to get orientation for this discussion of the results with red-wings. In addition to the quotations given earlier, the following summarizing statements are helpful: (p. 3) "The thesis of this essay is that the social group and its magnitude, in birds which are gregarious at the breeding season, are themselves exteroceptive factors in the development and synchronization of reproductive condition in the members of individual pairs of birds and throughout the flock." (p. 89)

"The group of fourteen present in 1937 was successful in breeding but it would be unwise to select any number . . . as being the numerical threshold. Six birds did not breed in one year; fourteen did in the next." (p. 105) "I feel drawn to speculate for a moment here on the fate of very small populations of animals. It is often found that when the representatives of a species in any one habitat are reduced to very low numbers, breeding becomes irregular and the species disappears in spite of careful efforts which may have been made to restore it."

The further discussion centers about Darling's ('38) three suggestions concerning the effect of size of local breeding populations upon the breeding activity and reproductive success of colonial nesting birds. As was stated before, Darling's suggestions were to the effect that in the larger colony breeding starts earlier, there is greater synchronization of egg-laying, and group survival values are shown primarily because of failure of very small colonies even to lay eggs or a reduced span of helplessness on the part of the eggs and nestlings. In addition, there is Stresemann's ('28) suggestion concerning a greater survival value of the larger colonies by mass protection against predators.

Relation of Colony Size to Onset of Breeding

Darling records that in 1936, the largest herring gullery (84–90 birds) which he watched began breeding 11 days before one with 20 birds while a colony of 2 pairs did not breed at all. In 1937, there was a lag of only 4 days between the largest colony and one of only 3 pairs, and the two larger colonies began breeding on the same day. In 1936, a colony of 72–80 black-backed gulls began breeding 8 days earlier than one of 18. The following year the difference was only two days between colonies of 120 and of 30 birds.

Roberts ('40) states that, in penguins, there appears to be no minimum threshold of numbers which is necessary to enable these forms to undergo a complete cycle of reproduction. A rough census of 137 colonies of Gentoo penguins (*Pygoscelis papua*) and Rockhopper penguins (*Eudyptes cristatus*), which ranged in size from 30 pairs to approximately 800,000 pairs, failed to give "any conclusive evidence that laying started earlier in the largest colonies, or that ovulation in the larger colonies was spread over a shorter period than in the small ones."

Fisher and Waterston ('41) have investigated the increase in numbers of breeding fulmars (*Fulmarus g. glacialis*) in the British Isles since 1878. It has been found that there is an average number of 4.4 years after a new breeding locality has been first populated by fulmars before any egg-laying is known. The possibility of a minimum threshold of numbers which is necessary for successful reproduction is suggested by these data. Egg-laying begins earlier in extensive than in small groups, although hatching and fledging tend to occur at about the same time in every colony.

Mayr ('41) investigated this point with red-winged blackbirds in four small swamps in New Jersey. In 1940 the five resident females in a brushy swamp laid their first eggs on May 20, 21, 22, 24 and 25 respectively. In a swamp with adequate cover, the 2 resident females laid their first eggs on May 24 and 25 or 26. In a similar swamp with one resident female, the first egg was laid on May 23. These data compare somewhat favorably with Darling's observations for gulls. A nearby larger swamp with poorer nesting sites but with a breeding population of 10–13 females, showed no red-wing eggs until May 26 or 27 (probable date). In my opinion Mayr has correctly interpreted the general situation to mean that ecological factors other than population size determined the earlier onset of breeding in the smaller as compared with the largest colony. With those colonies where the nesting sites are more nearly similar, Darling's generalization on this point has some support.

Similarly inclusive evidence is furnished by Fautin ('41b) who carefully followed the progress of nesting activities in two colonies of yellow-headed blackbirds in Utah. The larger colony contained 83 nesting females and about 35 males. Similar counts for the smaller colony were 40 and 12 respectively. Fautin says (p. 108), "The deposition of eggs began about the same time in both colonies." The first egg was recorded on May 7 in the larger colony and on May 8 in the smaller one. This difference of one day happens to be in line with Darling's generalization.

The writer's observations upon redwings indicate that egg laying began two days earlier in 1940 in one of the smaller breeding populations than in the large colony at Orland. In 1941 there was a difference again of two days, this time in favor of the larger population so far as initial egg laying was concerned. The onset of general breeding started decidedly earlier in the larger colony in 1941.

From such evidence, it is impossible to conclude that, in these two species of marsh-nesting blackbirds, the onset of breeding is directly related to colony size. While such a conclusion may yet be reached when enough data are collected, the sampling observations to date do not permit such an inference to be drawn.

The question of effect of colony size upon the beginning and synchrony of breeding activities is a part of the broader problem of the role of exteroceptive factors such as courting display in mating. Howard ('29, '35) has recently presented an explanation of the survival value of these activities. His theory is that display constitutes a normal type of extrinsic stimulation which intensifies sexual activity in a mated pair. If sexual activity is at a peak of intensity, a copulatory response may follow an ordinary stimulus of voice or appearance. Usually, however, an adequate synchronization of rhythms is obtained only by means of a further stimulus which is supplied by posturing. Frequently, if this stimulus is of subthreshold intensity, there is a summation of attempts which establishes a copulatory reaction whereas otherwise a delayed or unsuccessful coition might result. The importance of an effective synchronization of male and female reproductive rhythms is expressed by Howard ('29) who says that "those pairs . . . in which the rhythms of reactions combine harmoniously will score a larger number of successful conjugations" than other pairs in which there is a weaker manifestation of display and posturing. It is the characteristics of highly integrated pairs, therefore, that will be perpetuated in the breeding population by natural selection. Marshall ('36, '42) also states that it is in this manner that the survival value of sexual display and adornment probably operates.

Darling ('38, p. 20) expresses the view that "although the immediate mate of opposite sex may be the most potent excitatory individual to reproductive condition, other birds of the same species, or even similar species, may play a decisive role if they are gregarious at the breeding season. Without the presence of others the individual pairs of birds may not complete the reproductive cycle to the limit of rearing young to the fledgling stage." (p. 96) "This finding is in keeping with expectations based on *theory of numerical thresholds and social stimulation*" (italics mine).

Behavior factors which might influence the onset and synchronization of breeding in colonies of red-wings include (1) song, which may be effective at a distance since it may be heard on a quiet day for as far as two miles (cf. Nuttall, 1840, cited by Allen, '14). (2) The ordinary display of males by erecting feathers. (3) A spiraling and hovering flight by males which eventually ends in a zigzag descent into the marsh. Allen describes this accurately (p. 90) and continues: "A dozen or more birds may frequently be seen in the air at once, as they perform these evolutions. At this time, also, hovering at a much lower height is frequently indulged in. With a few quick strokes of his wings, the male vaults from his post into the air, and with quivering wings and flaming shoulders, gives vent to his pent-up passion in the 'scolding song.' " (4) The males drive resident females at first in a sort of frenzied pursuit and later follow her quietly.

Any effect of these various flying activities would be limited to the red-wings within visual range; vocalization might be effective at a greater distance. Such exteroceptive factors could operate in the beginning of breeding, in the pairing of individuals in similar phases of the reproductive cycle and in the synchronization of breeding processes within individual pairs of birds and throughout a flock.

RELATION OF COLONY SIZE TO SYNCHRONIZATION OF BREEDING

Darling's ('38) most convincing data, although by no means all of his information upon this point, have already been summarized. Roberts ('40) did not find convincing evidence that egg-laying in the larger colonies of penguins extended for a shorter period than in the smaller ones. On the other hand Fisher and Waterston ('41) record a slightly shorter period of egg-laying in large as opposed to small groups of fulmars. However, there do not appear to be any differences in the periods of hatching or fledging in relation to the magnitude of breeding population.

Fautin ('41b, p. 108) found that the duration of egg-laying in his larger colony of yellow-headed blackbirds lasted from May 7 to June 10; in his smaller colony, the limiting dates were May 8 to June 22. The duration of laying was 11 days shorter in the larger colony. Fautin (p. 119) does not regard this difference as conclusive support of what he terms "Darling's Principle." Emlen ('41) has studied with care the breeding behavior of the Tricolored Red-wing (*A. tricolor*) and, upon the basis of his own observations and those of others, concludes (p. 211): "Tricolored Red-wings probably also depend to a certain extent on mutual stimulation from colony associates, for members of each nesting group show a marked simultaneity in breeding which is completely lacking as between different groups."

The red-wings at Orland similarly showed a higher degree of synchronization of breeding activity in brood I during the earlier part of the breeding season (see figure 2). This is better seen if attention is focused upon the bulk of egg-laying. In group B there was a sharp rise in egg production between May 27–June 4, at which time there was a decrease in such activity at Orland. To be sure the *total* time span for ovulation was greater in the larger colony at Orland than in the scattered smaller populations. As the season progressed, however, the environmental conditions became progressively dissimilar in the lots under consideration to such an extent that by the middle of June size of population is a factor of doubtful importance, in comparison with other elements of environmental control. If this analysis is correct, available data do suggest a higher synchronization of egg-laying activities which was associated with the greater density of breeding population at Orland during an important part of the 1941 breeding season.

THE RELATION OF POPULATION DENSITY TO REPRODUCTIVE SUCCESS

From some points of view this is the crux of the entire matter, since it raises the question of possible evolutionary significance of population density in terms of survival values. Selection could favor either scattered or clustered nests or be entirely neutral as regards this factor. When or if the larger breeding population has survival value, this may result from the operation of one or more of the following factors: (1) tolerance for near neighbors in the face of a shortage of suitable nesting sites (cf. Allee, '31); (2) mass protection supplied by the "mobbing" of potential predators (cf. Stresemann, '28); (3) added protection on a percentage basis from the presence of larger numbers of prey (cf. Fautin, '41b); (4) heightened synchronization which shortens the more defenseless egg and nestling stages (cf. Darling, '38).

The present investigation has been concerned only incidentally with social tolerance. During 1940 and 1941 the red-wings did not populate all available cat-tail swamps to a certain toleration level and then overflow into marginal types of vegetation. Also in extensive cat-tail tracts which were studied in 1939, and which had contained a large population of nesting red-wings, the nests were not equally distributed but tended to occur in denser sub-colonies in the midst of less densely occupied areas of adequate cat-tail marsh.

As regards mass protection of eggs or nestlings, such behavior has long been recognized (cf. Stresemann, '28; Allee, '31). In the marsh at Orland, crows in particular were mobbed by grouped red-wings. The lack of cowbird parasitism at Orland in 1941 as contrasted with almost 5 per cent of parasitized nests in B may also be a measure of group protection. Since, however, the reproductive success was approximately the same in the different categories studied, such mass protection as existed was apparently offset by some unknown factor or factors.

It may be remembered that the only statistically significant difference in reproductive success was found in nests that were assigned in the field to brood II. In this brood approximately 30 per cent more young were fledged at Orland than from the scattered B colonies. These results seem to be related to physical environmental differences. More specifically, it is believed that this difference is related to a drying up of the smaller marshes and ponds during the latter part of the breeding season while the marsh at Orland still held much water. The higher figure of mortality of brood II in B may be directly due to an increased availability of these eggs and nestlings to predators as a consequence of this environmental trend toward a terrestrial type of habitat; or it may possibly be an expression of a decrease in attentiveness of adults during the latter part of the breeding season in marshes and ponds which are progressively becoming dry. Either of these causes would tend to increase the mortality of eggs and nestlings in brood II in B. A continuation of these relationships probably permitted the July eggs to be deposited at Orland while continued breeding in the smaller marshes was effectively discouraged by their deterioration as breeding habitats. Lack ('33), in connection with investigations concerning the breeding of Arctic Terns (*Sterna paradisaea*), states that egg-laying does not normally take place unless certain conditions concerning the site and neighborhood of the nest are satisfied. This drying up of the marshes in group B could have affected the survival of nestlings by diminishing the available food supply. Allen ('14, p. 101) states that red-wing nestlings are fed on insect larvae or imagoes obtained in the marsh. The importance of an increased scarcity of such food, if indeed it was a factor at all, is lessened by the fact that loss was more severe in the egg stage than among the nestlings and by the further consideration that no dead bodies of starved nestlings were found.

Thus there is no evidence left that the larger breeding population of red-wings at Orland showed an increased reproductive success which could be attributed to a higher synchrony of the breeding processes such as Darling ('38) observed for gulls.

Fautin ('41b, p. 118 ff.) found that the yellow-headed blackbirds which he studied hatched 75.7 per cent of 301 eggs laid in the larger colony as against 60.6 per cent of 142 eggs in the smaller colony. The larger colony was more disturbed by wind but the percentage of eggs destroyed, principally by predation, in the smaller colony was more than double that in the larger one. The final figure of success in producing fledglings was only 8 per cent greater for the larger colony. He discusses these results in connection with those of Darling's and adds the idea that the greater number of available prey in larger breeding colonies would tend to reduce the percentage lost by predation and so tend to give a higher survival value. This is true provided there are similar numbers of similarly effective predators in the situations which are being studied.

There is a possibility that even the best isolated pair of red-wings were not effectively isolated from other red-wings which were breeding in the general study area. If song is of importance in initiating and synchronizing breeding processes in these birds, and even though we halve the recorded distance which red-wing songs can be heard by man, none of the marshes studied was a mile away from larger breeding populations and many of them were within visual distance of other colonies with displaying males. The validity of this suggestion cannot be estimated from available data. It is a complicating factor which should not be forgotten.

COMPARATIVE STUDIES IN REPRODUCTIVE SUCCESS

An analysis of the fate of every egg deposited in groups A and B during the breeding season of 1941 indicates that, of 1140 eggs which were laid in 25 study localities, 675–681 individuals left nests as juveniles. This gives a mean reproductive success of approximately 59 per cent. This is rather high in comparison with numerous other published figures of reproductive success in red-wings. Nice ('41) has pointed out that there is no authenticity for a higher figure of 78 per cent which is cited by Kalmbach ('39) and Fautin ('41a) upon the basis of Allen's ('14) investigations of this species. Six other studies upon red-wings give figures of reproductive success which range down from the percentage here recorded. Incomplete results of Perkins ('28) indicate that 47 individuals, or 57 per cent, were fledged successfully out of a total number of 83 eggs in 24 nests of this species. M. Wood ('28) records a success of 21 fledglings (54 per cent) of 39 eggs which were deposited in 12 red-wing nests. In a neighboring swamp H. B. Wood ('38) found a success of 48 per cent from 73 eggs in a sample of 23 nests. Williams ('40) records 105 individuals, or 49 per cent fledged from 214 eggs deposited in 67 nests in a cat-tail marsh of about 10 acres in Ohio. These figures, gathered by different observers in diverse localities, are all of the same general order of magnitude.

Much lower nesting success has also been found in this species. Gabrielson ('15) on scanty data reports a success of only 8 nestlings, or 36 per cent, from 22 eggs which are known to have been deposited in 9 nests. Kalmbach ('39) records a very low figure of hatching of only 27 per cent in 281 eggs of red-wings in Louisiana; it is impossible that the percentage of fledging could have been in excess of 27 per cent. However, this reduced percentage of hatching is apparently explained by the fact that Kalmbach obtained his data in a locality where red-wings were breeding in abundance and where methods for their control were being worked out.

In a colony of yellow-headed blackbirds in Minnesota which was studied by

Roberts ('09), every egg or nestling in 36 nests was destroyed. The success of 130 eggs in this colony was thus nil. Fautin ('41a) in Utah found a success of 22 per cent in 443 eggs of the same species. These approach the values obtained by Gabrielson ('15) and Kalmbach ('39).

Nice ('37) has compiled data from 1994 eggs in six studies of reproductive success in a variety of open-nesting species of birds with altricial young. A mean percentage of fledging of 43 per cent was found in these studies. Nice's ('42) analysis of Kendeigh's ('42) compilation of reproductive efficiency for 2155 eggs in open nests of 11 species of altricial birds indicates a mean figure of success of 47 per cent in these latter investigations. Such data appear to suggest that red-wings reproduce somewhat more successfully than many other species of open nesting birds which construct their nests above ground level. This might be related to a lesser availability of red-wing eggs and nestlings to terrestrial predators which do not readily transgress an aquatic barrier such as is supplied by the borders of a marsh. However, this interpretation is not supported by the data on yellow-headed blackbirds which are also a marsh-inhabiting species. In addition, all such data, based on numbers of eggs laid, suffer from the serious lack of information concerning presence or absence of compensatory trends, such as might follow losses in early nestings.

The reproductive success found in this investigation in comparison with other studies upon red-wings may indicate an optimal set of environmental factors for red-wing reproduction during 1941 in the study area. There is a suggestion that any relation between population density and the reproduction of red-wings may have been obscured in the present investigation by such optimal conditions which existed for red-wings in breeding colonies of any magnitude. However, it appears that, if population density is a factor in the reproduction of red-wings, it must necessarily operate in association with numerous other physical or biotic environmental influences. Apparently, one or more of these factors may frequently be of greater importance than colony size in influencing the progress of reproductive activities or the survival of red-wing eggs or nestlings.

AREA AND EDGE

There is an absence of any correlation in this study of reproductive success with density of breeding population or with the extent of margin or "edge" in any of the study localities. In 1941 about 155 individuals bred in an area of approximately 5.0 acres at Orland. This indicates a fairly high density of population of about 31 individuals per acre. There was an aggregate number of approximately 12.8 acres in the 24 restricted marshes and ponds of group B. Since 157–163 individuals reproduced in these localities during 1941, there is a much lower density of about 12.5 individuals per acre in this category of marshes and ponds. Nevertheless, reproduction was apparently equally successful under such conditions of a relatively sparse density of breeding population. As was pointed out earlier, the 1940 breeding populations were of the same order of magnitude as in the following year.

Only round figures of edge in the various study localities have been obtained in this investigation. However, it has been found that there were approximately 3000 linear feet of edge between *Typha* and open water or between *Typha* and more mesophytic types of vegetation at Orland. This is a relatively slight extent of edge for an area of approximately 5.0 acres. It is what one might expect in a roughly rectangular marsh which is composed mainly of a dense, uninterrupted stand of cat-tails. In the marshes and ponds of group B there were essentially 16,000 linear feet of edge of various sorts.

Vegetational boundaries of such diverse types as those between buttonbushes and open water and between bur reeds and mesophytic grasses have been added in order to obtain this figure. This treatment is necessary at least in a preliminary survey in measuring a factor which is apparently as complicated as habitat margin or as edge. Beecher ('42) found a correlation between the number of linear feet of edge in a variety of types of plant communities and the distribution of nests of numerous marsh-inhabiting as well as other species of birds. There does not appear to have been a critical investigation concerning a possible relationship between the extent of edge in a locality and the success of reproduction of such forms. Insofar as this factor has been analyzed in the present study, there is no apparent edge effect upon reproductive success in red-wings.

In the present study a few other interesting results have been obtained. Some of these will be discussed briefly as an indication of certain environmental factors which appear to influence the success of reproduction in red-wings. At Orland, cat-tails constituted the supports and the concealing vegetation for every nest in which eggs were deposited during 1941. A variety of plants fulfilled similar functions in the 24 marshes and ponds of B, and reproductive success in 1941 varied widely among the study localities of this group in relation to vegetational differences. Table I shows that *Sparganium* comprised the cover of relatively few nests of red-wings in this category of localities. Among nests which were constructed in this type of vegetation, however, it has been found that reproductive success was only 25 per cent. An analysis of the data from nests constructed in *Typha* indicates a higher success of 59.9 per cent. This is approximately equivalent to the total percentages of reproductive success which were given for groups A and B (table III). The success of red-wing reproduction in two *Scirpus* localities and in a few brushy habitats of *Cephalanthus* and *Solanum* was in excess of 70 per cent. This high reproductive success is correlated apparently with the greater concealment of such nests. Among the various cat-tail marshes, there appears to have been less mortality in dense *Typha* localities than in open-water ponds in which the vegetation of cat-tails is reduced in extent or broken in its distribution. Approximately 56 per cent young were fledged successfully in nests which were built in open cat-tail situations while 63 per cent of the eggs in dense *Typha* localities were successful. These preliminary results strongly suggest a direct correlation of reproductive success with relative density of nesting cover among the various marshes and ponds of B and indicate a worthwhile problem for further study.

SUMMARY

1. The reproduction of an extensive breeding colony (A) of the Eastern Red-wing (*Agelaius p. phoeniceus*) has been compared with that of an equivalent number of individuals (B) breeding in small colonies in 24 marshes and ponds of restricted size.

2. The least synchronous total time span for ovulation was that of the colony of greatest magnitude. The total figures of reproductive success of groups A and B are essentially identical. These results are in contrast to those reported in gulls by Darling ('38).

3. Ovulation started earlier and there was a higher synchronization of the span of egg-laying of brood I in A than in B. These relations are similar to those found by Darling. However, the reproductive success of brood I was statistically similar in the category of smaller populations (B) and in the large population.

4. In brood II a higher one-day peak of ovulation in A than in B is again in conformity with Darling's results. In this case there was a longer span of egg-laying in A as well as similar per-

centages of double-broodedness in A and B. The success of reproduction of brood II was significantly higher in the larger colony.

5. There was a slight rise in egg production during July in the large breeding marsh. The reproductive success of the July eggs was very low.

6. No obvious correlation existed between reproductive success and the magnitude of breeding population in various minor groupings of the study localities of B.

7. The markedly higher success of reproduction of brood II in A than in B and the existence of a small July brood in group A are believed to be related to a drying up of the smaller localities during the latter part of the breeding season.

8. A mean reproductive success of 59 per cent is given which appears to be rather high in comparison with other published figures for altricial, open-nesting species which construct their nests above ground level.

9. There was an absence of any obvious correlation of reproductive success with density of breeding population per unit of area or with the extent of margin (edge) in the study localities.

10. A direct correlation of reproductive success with relative density of nesting cover among the various restricted marshes and ponds of B is suggested by preliminary results.

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CYPRESS–GUM COMMUNITIES IN THE BLUE GIRTH SWAMP NEAR SELMA, ALABAMA[1]

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Cypress–gum forests are common along the seaward margin of the Coastal Plain from Texas to Virginia. In addition, there are numerous stands in the low backlands of many of the streams in the interior of the southeastern states (Coulter, '04). Throughout the broad alluvial valleys these swamp forests are usually composed of bald cypress (*Taxodium distichum*)[2] and tupelo gum (*Nyssa aquatica*), whereas in pineland ponds they include pond cypress (*Taxodium ascendens*) and swamp black gum (*Nyssa biflora*) as the *predominant* species. In the shallow swampy areas of the lower portion of the Gulf Coastal Plain, slash pine (*Pinus caribaea*) may be an important associate of pond cypress and swamp black gum. Each of these five swampland species has been observed in pure stand. In some areas these species may occur as companion species, especially where pineland streams flow into broad river valleys.

The tupelo gum–cypress–swamp black gum and the tupelo gum–cypress forests investigated have been designated as variants of Cover Types Numbers 94 and 95 by the committee on forest types of the Society of American Foresters (Hawley, R. C. et al, '40). The following species have been listed as common associates: red maple (*Rufacer drummondii*), planer tree (*Planera aquatica*), pumpkin ash (*Fraxinus profunda*), water ash (*Fraxinus caroliniana*), and black gum (*Nyssa sylvatica*). These forests are of much importance economically since they yield timber crops on annually flooded soils in addition to harboring some of the most valuable and interesting animals indigenous to southern United States.

The stands herein reported are located in the Blue Girth Swamp in Dallas County, Alabama. This swamp is approximately 5 miles east of Selma and is in communication with the Alabama River 4 miles southwest of where the swamp is crossed by State Highway Number 14. The swamp is accessible by numerous field roads, the Southern Railroad, and a cable suspension bridge. Each of these approaches lies to the north of State Highway Number 14 (fig. 1).

Blue Girth Swamp lies in an elongated basin which is approximately 10 miles in length and averages about one-third of a mile in width. Most of the surrounding terrain is under cultivation, the major crops being cotton, corn, and peanuts. The swamp is spring-fed and possesses a nearly continuous hydroperiod. The average annual fluctuation during normal stream flow approximates 3 feet. Following excessive precipitation during April, 1938, the Alabama River experienced a rise of some 10 feet above flood stage with a corresponding rise in the water level of the swamp. Such a water level, however, is unusual in the Blue Girth Swamp.

In the swamp, stands of the tupelo gum–cypress complex are characteristic of the deeper waters (2–7 ft.), while samples of the tupelo gum–cypress–swamp black gum forest are found along the marginal areas in shallower waters (0–2 ft.). Pure forests of swamp black gum and marshes of bur-reed (*Sparganium americanum*) are present in the shallow waters south of State Highway Number 14. Contiguous stands of tupelo gum–cypress–swamp black gum, tu-

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[1] Contribution from the Botany Department, Tulane University, New Orleans, Louisiana. The authors wish to thank Mrs. Faith P. Mackaness for drawing the map of Blue Girth basin and environs.

[2] Nomenclature follows Small's Manual of the Southeastern Flora, 1933.

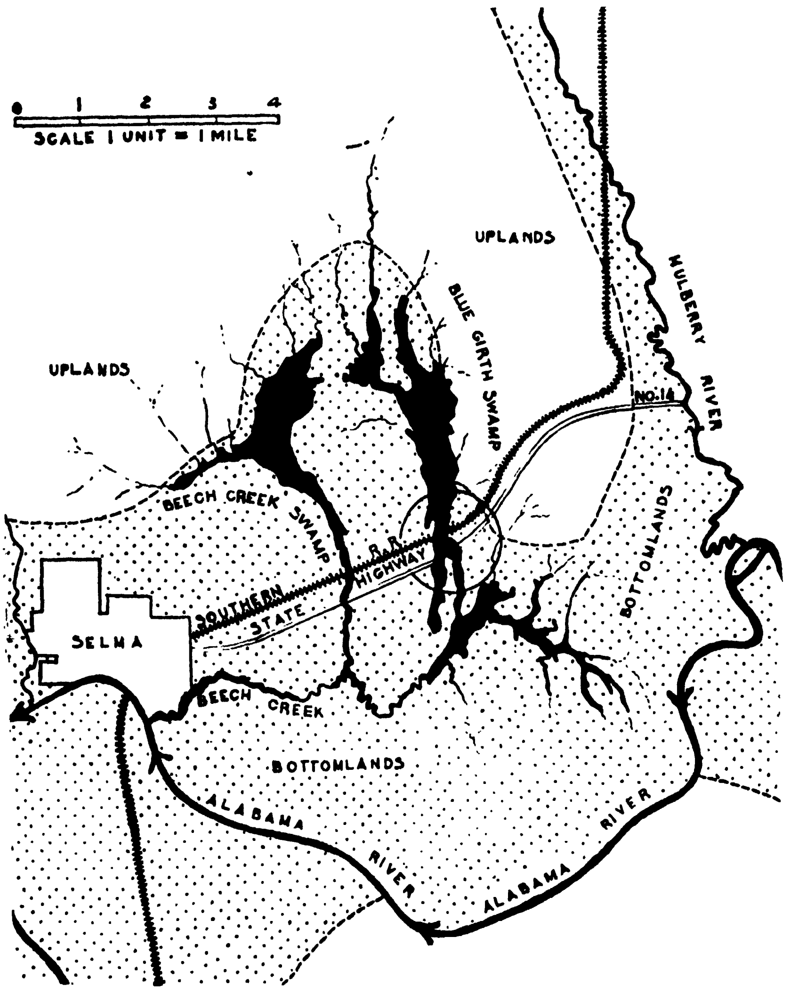

FIG. 1. The swampland communities investigated are situated within the encircled area of Blue Girth basin. Swampland communities shown in black.

pelo gum–cypress, and cypress forests were investigated. The communities are located in the proximity of the Southern Railroad trestle (fig. 1).

METHODS

The floristic composition of the arborescent stratum was determined by using twenty contiguous quadrats in each community. Each quadrat was 19 feet on a side and thus covered an area of 1/120th of an acre.

The numbers of trees, shrubs, and vines were recorded and the trees were distributed into two size classes (individuals greater than and less than one inch in diameter above the swollen base). The diameter of the swollen base (d. s. b.) was ascertained at a point about half way between the ground line and the bottleneck. The bottleneck is the point on a tree where the swollen base merges into the normal trunk. All measurements on the normal trunk were taken just above this point. This measurement is referred to as the diameter at the bottleneck (d. b. n.) Additional measurements, such as the height of the trees and the distance from the forest floor to the junction of the swollen base and normal trunk were obtained for each community.

The herbaceous understories were sampled by means of ten quadrats (each one square meter) arbitrarily spaced at five-meter intervals. The species occurring in each quadrat were recorded along with assigned cover values. Using a clipped lawn as a basis (100 per cent) the following coverage classes were utilized (figures representing percentages).

X = less than 1
1′ = 1 to 5
1 = 6 to 25
2 = 26 to 50
3 = 51 to 75
4 = 76–100

From the above data the frequency percentage of each species was obtained readily.

TUPELO GUM–CYPRESS–SWAMP BLACK GUM STAND

In the tupelo gum–cypress–swamp black gum forest towering, conical-crowned cypress trees 110 feet tall project well above the crowns of the tupelo gum. Below the tupelo gum stratum, the swamp black gum constituted a third layer up to 75 feet in height. This multistratified canopy shaded the water surface which was covered by a nearly continuous sheet of yellowish-green duckweeds (fig. 2). All the trees were slender, with conspicuously swollen bases encircled by dark green mantles of bryophytes. Except for the lowermost foot of the trunk above the water surface, bryophytes were confined mostly to the northern faces of the trunks but whitish-gray lichens extended well up into the tops of the trees. The understory presented a ragged appearance due to the poorly developed lower tree and shrub strata, as well as to a tangle of vines. Numerous conical cypress knees, up to thirty inches tall, projected a half foot or more above the water surface and still others were hidden from view. The dense sheets of duckweeds were interrupted repeatedly by the graceful floating leaves of the spotted pondweed (*Potamogeton pulcher*). In a shallow marginal strip approximately five feet wide, the spotted pondweed dominated the habitat almost to the com-

FIG. 2. The well-developed crown cover in the tupelo gum–cypress–swamp black gum forests casts a dense shade on the water surface which is covered by a nearly continuous sheet of duckweeds.

TABLE I. *Composition of swamp forest communities. Number of woody plants per acre*

Species	Tupelo gum–cypress–swamp black gum		Tupelo gum–cypress		Cypress	
	Greater than 1 in.	Total	Greater than 1 in.	Total	Greater than 1 in.	Total
Nyssa aquatica	300	348	342	462	48	498
Nyssa biflora	216	216	0	0	36	36
Taxodium distichum	36	120	96	96	252	252
Fraxinus pennsylvanica	24	108	0	0	0	0
Itea virginica	0	60	0	12	0	0
Cephalanthus occidentalis	0	60	0	30	0	0
Svida sp.	0	36	0	0	0	0
Smilax walteri	0	12	0	0	0	0
Smilax laurifolia	0	12	0	0	0	0
Totals	576	972	438	600	336	786

plete exclusion of other herbaceous aquatics.

Arborescent stratum

The tupelo gum–cypress–swamp black gum community studied included 972 individuals of woody species per acre (table I). Tupelo gum was the most abundant species with a total of 348 individuals per acre, and swamp black gum was next with 216 individuals. The trees of all species were distributed rather evenly throughout the community.

The diameter of the four species of trees varied considerably. Bald cypress presented the greatest average diameter with a value of 21 inches diameter at the bottleneck (d. b. n.) and tupelo gum and swamp black gum averaged 11 and 9 inches d. b. n. respectively. In general the diameter at the bottleneck was only one-half that of the swollen base.

As calculated from the data at the bottleneck (normal trunks just above the swollen bases), this community possessed the unusually high basal area of 402 square feet per acre. This high value is attributed primarily to the great number of individuals per acre. Of this total basal area, the component species contributed as follows: tupelo gum, 50 per cent; bald cypress, 25 per cent; swamp black gum, 24 per cent; and the remaining species one per cent. The basal area through the swollen bases was approximately three times as great (1188 sq. ft.). Since old growths of non-swamp timber rarely attain a basal area of more than 200 sq. ft. per acre (based on measurement at breast height), the magnitude of the above figures can be appreciated.

Tupelo gum and swamp black gum were the most frequent species (table I). A survey of the community revealed nine species not sampled in the quadrats. They are all common species of a fragmentary bottomland community which occurred along the margin of the swamp forest. Occasional specimens have survived in the swamp proper even though the hydroperiod is nearly continuous. Of these, three each are trees, shrubs, and vines: (1) *Magnolia virginiana*, *Rufacer drummondii*, *Salix nigra;* (2) *Alnus rugosa*, *Cerothamnus ceriferus*, *Styrax americana;* (3) *Decumaria barbara*, *Bignonia radicans*, and *Toxicodendron radicans.*

The total shade cast by the community was measured by determining the area of sun flecks at 12 o'clock on ten quadrats of one square meter each, and spaced at a predetermined interval of ten meters. An average value of 70 per cent of shade was secured in this manner, and it is believed that this represents fairly well the shade cast by both the crowns and trunks of the trees. Simultaneously, readings were taken in the shadier portions of the forest on a Weston foot-candle meter with the absorbing surface directed north, east, south, and west consecutively. The light intensity varied from 50 to 350 foot candles with 150 foot candles being most frequent.

Conical cypress knees were abundant (850 per acre) in the shallow water, and averaged about two and one-half feet in height. Gum knees, which are common in the swamps of southern Louisiana and Mississippi, were not observed in the Blue Girth community. In shallower spring-fed tupelo gum forests in northern Alabama only an occasional knee has been observed. These facts suggest that factors conducive to the production of gum knees are apparently different from those required for the production of cypress knees.

Herbaceous understory

The herbaceous synusiae included a multi-stratified mat of pleuston and the submergent community whose component species were anchored to the substratum. The floating synusia was characterized by an almost continuous sheet of a small form of the greater duckweed (*Spirodela polyrhiza*). This species was observed in open sunlight and shade in all communities in quiescent water (fig. 2). Quadrat studies revealed that the greater duckweed was the most important species of the community, with the floating moss-seed (*Bruneria punctata*) and the water fern (*Azolla caroliniana*) as minor associates. The exceptional total cover (more than 100 per cent cover) is attributed to the vertical stratification of the pleustonic species (table II). The infra-pleustonic species were found usually just below the rootlets of the greater duckweed. This horizon extended approximately one foot vertically and was composed of the following species in decreasing order of cover: the bog-mat (*Wolffiella floridana*), duckweed (*Lemma sp.*), small bladderwort (*Utricularia pumila*), and a liverwort (*Riccia fluitans*).

TABLE II. *Relative cover and frequency of herbaceous species in the tupelo gum-cypress-swamp black gum swamp and the bur-reed marsh in the Blue Girth swamp.*

	Swamp		Marsh	
	Cover class	Frequency per cent	Cover class	Frequency per cent
Emergents				
Potamogeton pulcher	1	100		
Persicaria hydropiperoides	X	60		
Nama quadrivalve	X	60		
Sparganium americanum			2	100
Saururus cernuus			X	40
Pleuston				
Spirodela polyrhiza	4	100	3	100
Bruneria punctata	X	100	1	100
Utricularia pumila	1′	100	X	100
Wolffiella floridana	1′	100	X	20
Lemna minor	X			
Lemna sp.	1′	90	X	20
Azolla caroliniana	X	40		
Riccia fluitans	X	40		
Submergents				
Myriophyllum pinnatum	1′	100	X	10

Among the anchored aquatics, the spotted pondweed (*Potamogeton pulcher*) was the predominant species. Watermilfoil (*Myriophyllum pinnatum*), smartweed (*Persicaria hydropiperoides*), and waterleaf (*Nama quadrivalve*), were the only other frequent species but the coverage of each was meager (table II).

Epiphytes were common on the three species of trees. Spanish moss (*Dendropogon usneoides*), approximately at the

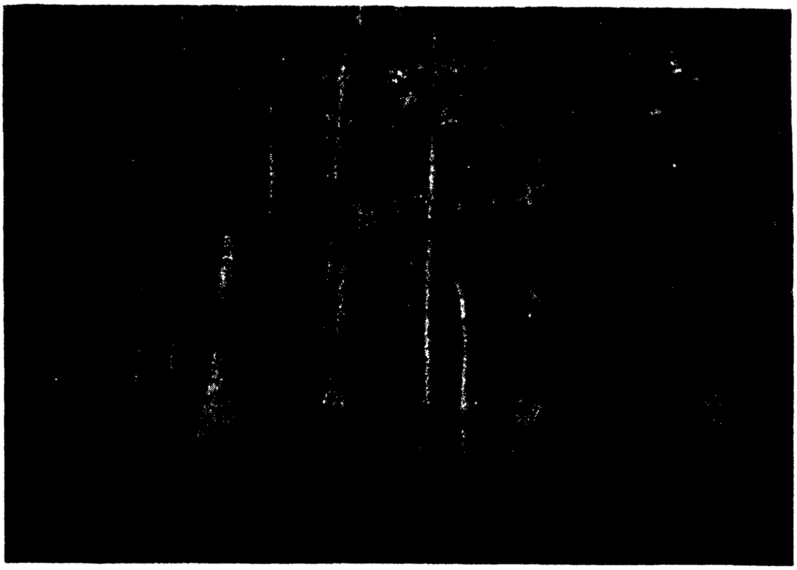

FIG. 3. Dense sheets of duckweeds are lacking in the tupelo gum–cypress community where stream flow is perceptible.

northernmost limit of its range in the interior of the United States, festooned some of the cypress trees but was sparse on both species of gum. Settlements of the polypody fern (*Polypodium polypodioides*) and specimens of the beard moss (*Usnea sp.*) were observed occasionally on the more suitable surfaces of the tree trunks but neither was abundant.

TUPELO GUM–CYPRESS STAND

The tupelo gum–cypress stand investigated occurred in somewhat deeper water than the marginal tupelo gum–cypress–swamp black gum forest described above. The soil surface near each tree, however, was elevated as much as one foot above the surrounding forest floor. In places streamflow was perceptible and under such conditions no pleustonic forms were in evidence (fig. 3). However, the cool, very clear water was well populated by the water-milfoil and the delicate-leaved pondweed (*Potamogeton pusillus*) which together formed a veritable water garden.

The physiognomy of the tupelo gum–cypress stand was similar to that of the tupelo gum–cypress–swamp black gum community. The tall slender trees possessed the same swollen bases blanketed near the water level with bryophytes (fig. 3). The upper trunks and branches also were characterized by few bryophytes but abundant lichens and an occasional settlement of the polypody fern, the mistletoe (*Phoradendron flavescens*), and the Spanish moss. Cypress knees were present in the shallower water but no tupelo gum knees were observed.

The tupelo gum–cypress stand differed somewhat from the more marginal community. The number of trees per acre was less (600 *vs.* 972) and the basal area (sq. ft. per acre) was somewhat lower (336 *vs.* 402). The per cent of shade was also somewhat less (60 *vs.* 70).

Perhaps the most important feature of this swamp forest was the abundance of floating logs. The logs were restricted mainly to the deeper portion of the swamp since the numerous cypress knees impeded their movement into the shallow water. These logs were populated by a number of mosses and wetland herbs. From a distance these floating settlements appeared like haphazard, green fence rows running through the swamp. The predominant angiosperm species of these unique settlements was the St. John's wort (*Triadenum petiolatum*). Common associates were tickweed (*Bidens discoidea*), false nettle (*Boehmeria cylindrica*), water hoarhound (*Lycopus rubellus*), pennywort (*Hydrocotyle verticillatus*) and blackberry (*Rubus sp.*). Most of these same species also colonized the swollen bases of the dominant trees. Colonization was not very successful, however, presumably due to the alternate periods of flooding and dewatering due to the natural fluctuation of water level in the swamp.

CYPRESS STAND

The cypress stand investigated included the cypress as the predominant species. In appearance this stand differed little from the tupelo gum–cypress–swamp black gum and tupelo gum–cypress communities. However, the cypress trees were larger and more numerous, and contributed 76 per cent of the total basal area. Striking characteristics included the flaring buttresses of the cypress trees and an abundance of pinkish to gray lichens on the cypress trunks. The cypress knees were much taller than in the marginal community, presumably due to greater depth of water in the cypress stand.

As in the tupelo gum–cypress community there were numerous, partly submerged logs inhabited by wetland herbs. Species unique to these settlements included luxuriant specimens of the cardinal flower (*Lobelia cardinalis*) the skullcap (*Scutellaria lateriflora*) and the infrequent loosestrife (*Decodon verticillatus*). When the cardinal flower was in full bloom this scene was a very attractive swampscape.

SOILS OF SWAMP FORESTS

The swamps were traversed readily on foot, as one rarely sank above the ankles on the relatively firm swamp floor. The forest floor contained a well-developed horizon of litter eight to twelve leaf layers thick, below which was a stratum of decaying organic matter. Typically, this peaty material extended to a depth of one foot, was matted with myriads of rootlets, and contained an abundance of tupelo gum seeds. Below this highly organic horizon was a stratum of blue-gray, sandy clay mottled with yellow or brown and nearly devoid of organic material. These observations on the firmness of the forest floors are supported by the data on water content. Although the water content in the first foot of soil was moderately high (2.26 to 2.97 times the oven-dry weight), that of the second and third feet of the substratum was comparatively low (0.19 to 0.26 times the oven-dry material). This indicates a very low water-holding capacity and contrasts markedly with the water content at saturation at similar levels of swamp soils in the lower Gulf Coastal Plain which contained 15 to 20 times the moisture here noted (Hall and Penfound, '39).

The hydrogen-ion concentration was determined for the soil samples that were utilized in the study of water content. Eight aliquot sub-samples were tested for each horizon at each soil sampling station by means of a LaMotte-Morgan colorimetric soil testing set. The pH values in the respective horizons of the three communities were found to be similar so that a general value for each depth was obtained. The peaty surface foot yielded a value of pH 5.3 most frequently but the sandy clays of the second and third foot samples were at pH 6.0 most often. Since more than 90 per cent of the rootlets occurred in the upper foot of decaying organic matter, the hydrogen-ion concentration of this horizon is more important ecologically than that of any other horizon. These are the most acid conditions under which tupelo gum, a supposedly neutrophilous species, has been encountered (Penfound and Hathaway, '38), (Penfound and Hall, '39).

The hydroperiod in Blue Girth Swamp is almost continuous. The depth of water varies with the community and presumably is a major factor in the distribution of the dominant species. The marginal forest containing swamp black gum extended into water as much as one and one-half feet in depth, whereas the cypress–tupelo gum communities usually occurred in deeper water (1.5–5 ft.). These facts suggest that the limiting factors in the distribution of swamp black gum at Blue Girth are related to the depth of water.

BUR-REED MARSH

The sample of the bur-reed marsh investigated lies to the south of Alabama Highway No. 14 (fig. 1). The community occupies a tract of land approximately one-half mile in length and one-fourth of a mile in width. Although this marsh area is meager as compared to the coastal marshes, it represents the largest stand of *Sparganium americanum* observed by the writers. Therefore, a brief description of the community is deemed advisable.

The bur-reed marsh occupies a shallow basin which is surrounded by a fringe of the gum–cypress forest in which the swamp black gum (*Nyssa biflora*) is predominant (fig. 4). In the marsh proper, scattered specimens of bald cypress (*Taxodium distichum*) are fairly common, although most individuals are pole trees or of a smaller size class. Except for occasional cypress trees and a few small lagoons, the marsh has a uniform physiognomy (fig. 4). The lagoons in the marsh are formed when mats of bur-reed plants are floated out *en masse* following periods of intense precipitation. Such was observed in April 1938, and August 1939. During these months the total rainfall at Selma for the two-week period preceding each crest stage of the Alabama River was recorded as 18.55 inches and 15.85 inches, respectively.

The marshland vegetation was sampled by means of ten quadrats of one square meter each. *Sparganium americanum* was the all-important anchored aquatic with a frequency of 100 per cent and an average cover grade of 2. *Saururus cernuus*, the only other attached emergent herb encountered, had a frequency of 40 per cent even though its average cover was less than one per cent. *Myriophyllum pinnatum* was a common species in the shallow water but had only meager coverage (table II). In the

FIG. 4. The bur-reed marsh is interrupted by occasional small lagoons and dotted with cypress trees.

marsh, as in the swamp, mats of pleuston were well developed and the component species were identical with those previously recorded for the three cypress–gum forests. The greater duckweed (*Spirodela polyrhiza*) was the predominant species. The moss-seed (*Bruneria punctata*) was also abundant, especially in the open sunlight. Infrequent species, typically marginal in nature, included: *Typha latifolia*, *Rynchospora corniculata*, *Carex lupulina*, and *Scirpus cyperinus*.

The marsh was relatively soft and one usually sank to the knees in the loose organic matter to the firmer soil below. The top eighteen inches of marsh floor, aside from rootstocks, was composed of almost pure peat. At lower levels, a blue-gray sandy clay mottled with yellow was encountered which contained a small amount of decaying organic matter. Aside from the slight increase in the thickness of the layer of organic matter, the substratum of the marsh was strikingly similar to the forested area. The peaty character of the upper foot of soil is reflected in its high water-holding capacity (1383 per cent, as based on dry weight). The water-holding capacity at the second and third foot levels were 49 per cent and 40 per cent respectively, or approximately twice that in the forested areas.

The hydrogen-ion concentration was determined for samples of soil from three levels as well as that of the surface water. The samples from the first and second foot levels were at pH 6.0 most frequently which was identical with that obtained for the surface water. However, the soil from the third foot level was more acid (pH 5.4).

PHENOLOGY

Growth of the deciduous forests of the Alabama River Valley is well underway by March first. However, it is early April before the swampland communities are fully in leaf. Tupelo gum and swamp black gum were observed in flower during the first week in April. At this time most of the leaf buds of gum were open as were those of bald cypress. Thus it is seen that the leaf buds of the three major woody species open at approximately the same time. By July, well-developed fruits were abundant on the tupelo and swamp black gum trees. Although mature fruits and seeds from the previous year's crop were abundant on the water surface and forest floor, only a few first year seedlings were noted. Termination of the growing season usually occurs by the middle of October.

Many species of minor importance were flowering during the first week in April along with the predominant woody species. These plants included: *Itea virginica*, *Phoradendron flavescens*, *Potamogeton pulcher*, *Salix nigra*, *Smilax laurifolia*, *Smilax walteri*, and *Svida* sp. By the first week in June, *Saururus cernuus* had reached the height of anthesis, and well-developed fruits were present on *Potamogeton pulcher*. A month later most of the fruits of the latter species had been disseminated, whereas the ripe spikes of the former species were retained until the fall.

BIOTIC FACTORS

Blue Girth Swamp provides recreational facilities to fishermen and hunters in the vicinity of Selma. It is undoubtedly one of the best wildlife areas of Dallas County, since here one encounters such species as the alligator, beaver, swallow-tailed kite, pileated woodpecker, wood duck, and anhinga, all of which are inhabitants of the primeval swamp forests of the lower Gulf Coastal region.

Cattle have been observed grazing on palatable forbs on the ridges which border the swamp. In July when flies of the genus Chrysops were present in abundance the cattle retreated to the swamp since the adult flies do not occur abundantly in the cypress–gum communities. Apparently, the swamp herbs are not very palatable to the cattle since grazing in the swamp was not observed.

Relatively narrow corridors have been cleared across the swamp for railroads, highways, and power lines. These areas, where shallow, are occupied by bur-reed marshes. A small amount of selective cutting has been done and some of the larger cypress trees have been removed apparently to supply the needs of the inhabitants living in the vicinity of the swamp. These activities of man have had only a minor influence since they are localized and are of insufficient extent to be detrimental to the area. In general, it is believed that man and his domestic animals have exerted little influence on the vegetation of these swampland communities.

SUMMARY

The Blue Girth Swamp, near Selma, Alabama, is a spring-fed swamp about ten miles long and approximately one-third mile in width. It is often flooded by backwaters of the Alabama River. The average depth of the water varied from a few inches on the margins to over four feet near the middle and apparently is the limiting factor, either directly or indirectly, in the distribution of the dominant arborescent species.

This swamp included two arborescent types; a tupelo gum–cypress–swamp black gum forest which occupied a small portion of the shallow swamp margin; and the tupelo gum–cypress complex, which was composed of the tupelo gum–cypress associes and the cypress consocies. Small stands of bur-reed marsh also were characteristic of the swamp border.

The arborescent communities were characterized by a stratum of tall, slender trees; by the absence of small tree, shrub, and emergent herbaceous strata; and by an abundance of pleustonic, floating-leaved and submergent aquatic herbs. All the trees possessed swollen bases, which were usually clothed with a mantle of bryophytes, polypody fern, an occasional mistletoe, and sometimes with Spanish moss. Cypress knees were present in all communities but gum knees were not observed. Floating logs, which were common throughout the swamp, harbored numerous terrestrial and wetland species not found on the swamp floor.

The tupelo gum–cypress–swamp black gum, the tupelo gum–cypress, and the cypress communities were all characterized by an unusually large number of trees per acre (576, 438, and 338, respectively). Furthermore, they possessed a very high basal area as determined at the bottleneck (481, 336, 409 sq. ft. per acre, respectively). These figures are more than twice those for old growth stands of upland timber.

The bur-reed marsh occurred in pockets in the tupelo gum–cypress–swamp black gum swamp and was usually dotted with invading cypress trees and numerous small lagoons. The marsh was characterized by a soft peaty substratum with a very high water-holding capacity.

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THE EFFECT OF TEMPERATURE AND LIGHT ON OXYGEN CONSUMPTION AND RATE OF DEVELOPMENT OF HELISOMA

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INTRODUCTION

Purpose.—The backround of all ecological work dealing with fluctuations in animal numbers and resulting population changes is laid in the analysis of environmental factors producing such fluctuations. Most of these factors are not simple, but rather are of a complex nature, representing the interaction of such variables as temperature, humidity, light, evaporation, etc. to produce greater or lesser fecundity, resistance to disease and to competition, and in some cases greater or lesser velocity of growth or development at a critical period in the life history, all of which influence population. Of the physico-chemical components of the environment, radiation within the range of wave lengths referred to ordinarily as light has received relatively little attention. The evidence which has been offered in many cases was gathered incidentally to other research.

Most of the literature dealing with the problem of the effect of radiant energy of the visible spectrum upon rate of development or rate of growth was done previous to 1900 and suffers from the lack of adequately measured and controlled laboratory techniques. Recent work on radiation has been largely with the wave lengths above 700 mμ or below 320 mμ. In the analysis of natural conditions the latter radiation plays a relatively small part.

Beginning in 1934 and on the basis of preliminary work done in 1932 and 1933 on *Physa gyrina* the experiments covered in this paper were designed to determine:

1. The relationship of temperature to velocity of growth in *Helisoma trivolvis pseudotrivolvis* (F. C. Baker), considering only the period from fertilization to hatching of the egg;
2. What effect upon the temperature-velocity curve, if any, could be observed when the embryos developed under the light passing through various filters;
3. The oxygen consumption of the eggs during the developmental period, and,
4. Some of the relationships between light, temperature and oxygen consumption.

Literature.—Beginning with Edwards (1824) who claimed that tadpoles showed no development in the dark, and continuing through the work of Rugh ('35) who found no effect of wave length of light on development of frog tadpoles, the literature on the subject has contained almost every possible viewpoint on light-growth or light-development relationships. As Rugh and others have pointed out, probably most of the inconsistency is due to lack of control of other variables and the failure to distinguish between luminous intensity and radiation. Higginbottom (1850, 1863) found no differences in growth rates of tadpoles raised in light and dark. Beclard (1858) working with the larvae of *Musca carinaria*, reported that larvae grown in violet light, grew to be three times the size of those grown in green light. The sequence of colored lights, producing larvae in order of size from large to small, was violet, blue, red, yellow, and green. MacDonnell (1859) found no differences in the size of tadpoles raised in darkness and in light.

Schnetzler (1874) reported a slight retardation of growth in darkness. He also worked with tadpoles. Yung's papers (1878, 1880, 1892) have been the most extensive and consistent of any in the literature. This author used tadpoles of *Rana temporaria* and *R. esculenta*, eggs of *Salmo*, *Loligo* and *Lymnea*. He concluded that red and green light retarded growth, that darkness and yellow light had a negligible effect and that blue and violet accelerated. The order of effectiveness upon growth, ranging from greatest to least, was violet, blue, yellow, white, dark, red, and green. The tadpoles raised in darkness showed an increase in size over those raised in light, at thirty days, of 25 per cent, but at sixty days, this increase had been reduced to a difference of only 6 per cent. Yung secured his colors by means of chemical and dye solutions into which the containers of eggs and larvae were placed. These were aqueous Parma Violet (violet), alcoholic Lyons Blue (blue), aqueous potassium chromate (yellow), alcoholic basic Fuchsin (red), and aqueous nickel nitrate (green).

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[1] Thesis submitted for the Doctorate at the University of Illinois, 1937.

Yung's work has been criticized by Rugh ('35) on the following points:

1. With the exception of the green filters, the light was not monochromatic.
2. No attempt was made to control the heat source, which alone could account for the difference in growth.
3. The light source (sky) was unreliable and weak.
4. Plant food also grew poorly in green light and could account for the decline of the tadpoles.

Fatigati (1879, after Vernon) reported that violet light accelerated the development of infusorian cultures and green light retarded them. In extensive studies of environmental effects on development of echinoderm larvae, Vernon (1895) measured the lengths of the calcareous skeletons of the body and limbs of eight-day-old larvae which had been raised in various colored lights. Bacterial growths in violet light prevented the larvae from reaching the eight-day-old stage. Only semi-darkness produced animals with a greater body length than the controls. Other light conditions all caused a decrease in body size, the greatest decrease being in yellow light. The order given was, absolute darkness, blue (copper sulfate), green, blue (Lyons Blue), red, and yellow. The red and yellow lights were secured by means of photographic papers. Colton ('08) working with *Lymnea columella* states, "Darkness is prejudicial to growth." Animals grown from 45 to 54 days in light were from 25 per cent to 60 per cent larger than those grown in darkness. He states, however, that the plant food required by these animals complicates the problem of raising them in darkness.

Corradetti (1933) found that the larvae of *Rana esculenta* develop more rapidly in darkness than in white light or green light. Rugh ('35) reviewed the literature on the subject, repeated Yung's work with colored light to the extent of measuring the energy transmission of the solutions used by Yung, and reports finding no significant difference in the development of frog eggs raised in sunlight, blue, green, yellow-red, infrared and diffuse light (control). He used Corning glass filters, subjecting the eggs to daily, equivalent amounts of radiation based upon an intensity-time product and returning them to diffuse light between exposures. One of the valuable portions in his discussion is that regarding the distinction between radiant energy, wave length, and visible intensity.

Hammond and Titus ('41) found that neither color nor intensity of light had any subsequent effect on weight, egg production, fertility or hatchability of eggs of chickens exposed to various colored lights. The chickens were exposed to radiations of low intensity during the first sixteen weeks of life.

Blum ('41) has made an excellent summary of the literature dealing with certain photobiological reactions and a discussion of the problems involved.

As he points out, experiments dealing with radiation as illumination either involve a visual mechanism in the reacting organism or cannot be verified due to an absence of data on the energy distribution at various wave lengths of the filters or light sources used.

To summarize, the following points stand out:

1. A sharp difference of opinion exists as to whether or not light of the visible spectrum has any effect at all on development and growth.
2. In those experiments reporting an effect of wave length, green light has most consistently been found to retard the growth or the rate of development.
3. The data on the relative effects of other spectral regions are conflicting.
4. Much of the reported work fails to measure adequately or control other variables involved. The work is beyond evaluation because of lack of information as to transmission of filters, and radiant energy available to either larvae or embryos.

Definitions and basic theories.—It was thought that an analysis of the temperature-velocity relationships under various light conditions might be a useful approach to the problem by providing data on the effect of light upon thresholds and developmental totals. With this in mind the data were collected so that a temperature curve could be drawn for at least a portion of the range under each light condition.

Shelford ('27) and others have shown that the summing of temperatures to predict velocity or rate of development, which was done by many early investigators on the assumption that the time-temperature relationship is entirely represented by an equilateral hyperbola, is incorrect. The velocity of development does, in part, at medial temperatures, when plotted against the temperature give a straight line. Temperature bears a fixed relationship to velocity only within the limits of this line. The entire actual curve flattens out at the lower end either as a straight line relationship or as a curve, placing the true threshold below the hyperbolic zero, which may be called the theoretical zero of development. At higher temperatures the curve falls off at rates varying with the species. The actual threshold is a statistical point and not fixed, because differences in taxonomic variety or slight variations in physiological condition change the specific degree at which temperature begins to affect development. It is therefore necessary in measuring rate of development to define a unit which may be applied to the entire curve. Shelford defines this unit for any organism which shows a straight line portion of the velocity curve and says, "The developmental unit is the difference in the hourly velocity of development (based on the time to complete the stage), at two mean temperatures varying at approximately one degree per hour in the medial range." A modification of this definition was necessary to utilize the term developmental unit in these experiments, because the temperature variation was not regularly one degree per hour. Therefore the developmental unit is defined for these experiments as the difference in the hourly velocity of development (based on the time to complete the stage), at two mean, medial temperatures differing by one degree centigrade, these two being averages of the hourly temperatures during the time necessary to complete the stage. In this investigation, the medial range of temperature is at least 15° to 28° centigrade.

The following are definitions of terms used in this paper, most of which are from Shelford ('27, '30) and from an unpublished Bachelor's thesis offered at the University of Illinois in 1933 by the author:

The *threshold* of development is "the intensity or quantity of any factor immediately above which development begins to be measurable." In these experiments the actual threshold is the degree of temperature directly above which the amount of development is perceptible. It is not a fixed point, but has been shown to vary with other factors such as the chemical constituents of the water, the species, the individual, and the factors mentioned above as related to the rate of development, and as these experiments show, with the kind of light. The *alpha* referred to is the point of intersection of the prolonged straight line portion of the curve with the temperature axis, corresponding to the hyperbolic zero of those who summed temperatures. It is valuable for use in the calculations necessary for plotting the velocity curve.

The *developmental total* for any stage is "the sum of the developmental units for that stage." These totals vary with factors other than temperatures as shown in this experiment.

The *time* for the stage of development studied is the number of hours from the time of the laying of the egg mass to the median of the hatching times of the developed organisms under experimental conditions.

Velocity values (numbers of developmental units per hour for different combinations of temperature and light conditions) are regarded as standard for average experimental organisms, as was done by Shelford. This is more convenient in calculations than to regard the developmental total as a numerically fixed constant.

In graphic representation, *alpha* is again defined as the theoretical zero of development. The product of the ordinates and abscissas of any point on an equilateral hyperbola equals a constant, and the plotting of the reciprocals of the developmental time in hours (ordinates) multiplied by this constant on ordinates gives a straight line which crosses the temperature axis at an angle of 45° at a point equal to the hyperbolic zero. This point is the theoretical zero of development, *alpha*, and is consistent with the definition previously given in that the straight line portion of the velocity curve coincides with the straight line of the equilateral hyperbola above described.

Von Oettingen's method of finding the *alpha* value was to assume a series of values and calculating the various time-temperature products to select the one that gave the most nearly constant product for various temperatures. *Alpha* may also be calculated by the formula $(x - alpha)y = k$, where x is the temperature and y is the time. The use of the phrase "effective temperature" refers to the actual temperature minus *alpha* and applies to the straight line portion of the velocity curve, so that in calculating the time-temperature products, the effective temperature is used.

Because of individual variation, in most of the experiments a large number of eggs was used to arrive at dependable averages. The results can be significant only upon statistical analysis. All means were weighted to compensate for the unequal number of eggs used in the various experiments.

The frequency of recording data is an important factor in the evaluation of experimental results. Due to the time involved to complete the stage at low temperatures, a routine permitting tests every two hours, day and night, was not feasible. Also, the actual running of oxygen tests, measurements of rate of flow, temperature recording, standardization, etc., required considerable time. The records were taken on the average of every four to five hours.

Acknowledgments.—The author wishes to acknowledge his great indebtedness to Dr. V. E. Shelford, under whose direction this work was done. Valuable suggestions on the handling of the snails were made by Dr. H. J. Van Cleave. To the many fellow graduate students and friends who assisted with the experiments and from time to time made helpful suggestions on the treatment of the data my sincerest thanks are extended. Appreciation is also expressed

to the members of the staff of Western Reserve University for the use of the library and other facilities during the writing of this thesis, to Case School of Applied Science for use of equipment, and to the Nela Park Laboratories of the General Electric Company, Cleveland, for measurements of energy output of the lights used.

Methods and Procedures

Source of material.—The snails used in this experiment were *Helisoma trivolvis pseudotrivolvis*, a geographic race, named and identified by F. C. Baker and collected from a pond northeast of Urbana, Illinois, near the type locality. In the fall of 1935, this pond, designated Pond 7 in a series used for class study, was found to have a very large snail population. Large numbers of individuals were collected in October and November and brought to the laboratory. It was felt necessary to have the experimental material as uniform as possible, so measurements were made to ascertain whether or not the individuals collected could be said to represent a single population and a single group. The distribution in size around the mean of 15.722 ± .031 mm. for the greatest diameter is shown graphically in figure 1 Observations on rate of shell size increase made it evident that the differences between the peaks of this curve were too small to indicate any significant differences in age. This being so, the unimodal curve indicates that the population is a single age group, i.e. from eggs produced within a single laying period. After being measured the snails were placed in battery jars located in ice boxes and cold rooms at from 5°–8° C. where they were left until needed for experimental work. Food was supplied by placing fresh lettuce leaves in the con-

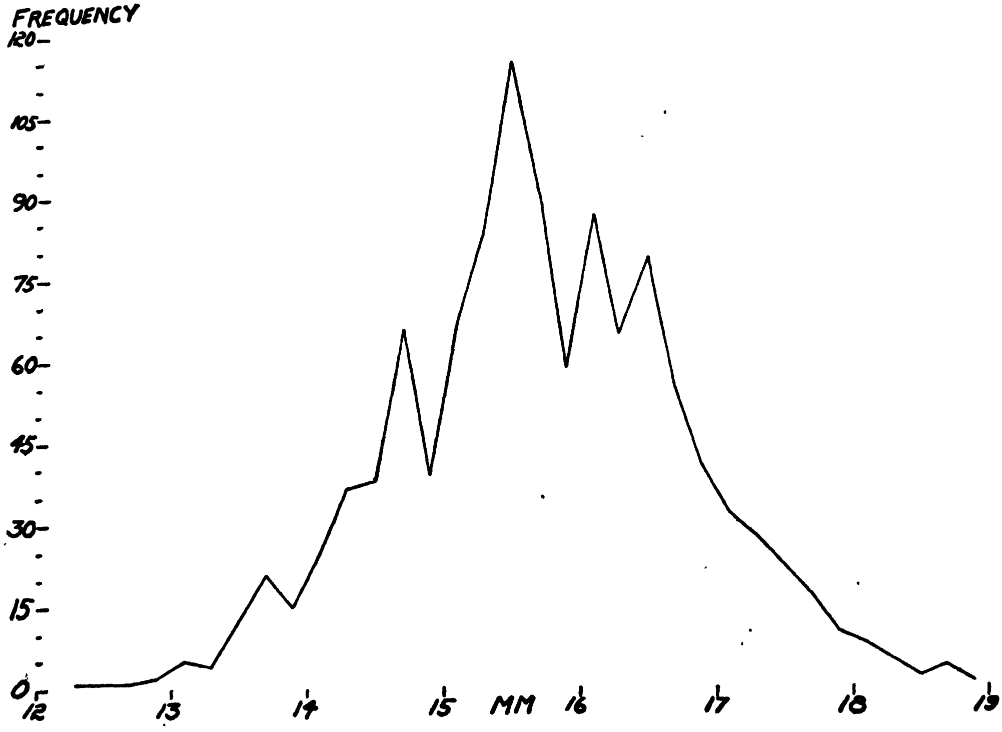

FIG. 1. Frequency distribution of greatest diameter measurements of 1,134 *Helisoma*. $\bar{m}$ = 15.722 ± .031 mm.; σ = 1.048 mm.

tainers about once a week. Water lost by evaporation was replaced from a container kept at the same temperature. These snails never laid eggs until brought out to room temperatures. The mortality was low until the early part of June, 1936, when the snails began to die rapidly.

At the same time a large number of individuals was placed in a tank in a glass-roofed house to provide a laboratory stock in case the field material became scarce. These snails multiplied rapidly and required no care, aside from feeding with lettuce. It was found that the snails of this stock were a satisfactory source of eggs when placed in battery jars, cooled gradually, and left for more than two months at the lower temperatures. Upon being brought back to room temperature following such treatment, copulation occurred and eggs were laid within 36 to 48 hours.

Preliminary experiments upon *Physa gyrina* and *Helisoma* had shown that animals brought from lower (below 10°) to higher temperatures would copulate and lay within 36 to 48 hours. The differences in time of laying were apparently related to the rate of warming. Practice made it possible to secure a large number of eggs almost on demand. The experimental animals were from both stocks. Repeated examination showed that the eggs were always uncleaved when laid and that all eggs within a single mass were at the same stage of development.

More than 150 eggs were measured and found to have a mean diameter of 1,097.4 μ, with a range from 973 μ to 1,176.0 μ. This measurement includes the egg membranes and semi-fluid material surrounding the fertilized egg cell. It is the diameter of the capsule within which the developing embryo appears to move freely. The zygote itself measures around 150 μ in diameter and shows less variation in size than the capsule. The number of eggs per mass varied from 3 to 34. The average number was 13.6. More than 5,000 eggs were collected for various purposes during the course of the experiments.

The water used in the laboratory and in these experiments came from the University water supply, which was run through a large carbon filter to remove excessive iron and chlorine.

Experimental apparatus.—The design of the apparatus for these experiments grew out of a consideration of the following points:

1. The water supply must be continuous to provide oxygen and water for sampling without disturbing the eggs;
2. The temperature of the water must be controlled;
3. Chemically, the water must be identical in all experiments;
4. The pressure upon the eggs must be uniform;
5. A number of experiments must be run simultaneously under the same light conditions, but at differing temperatures;
6. The radiation available must be measured and kept as constant as possible;
7. The eggs must be visible at least part of the time in order to record hatching time;
8. Light must fall upon the eggs as uniformly as possible and from as many directions as possible, and,
9. The radiation intensity must be higher than that provided by various devices for securing monochromatic light.

The apparatus shown diagrammatically in figure 2 was constructed as coming close to meeting all the requirements. The single source from the carbon filter was used to pass water into a heating tank on the floor above and also into a cooling pipe surrounded by brine and located near the apparatus. The hot and cold waters were then passed into pressure bottles and the levels adjusted to supply equal pressure. From here, glass and rubber tubing led to a series of eight mixing bottles, each supplied with hot and cold water and

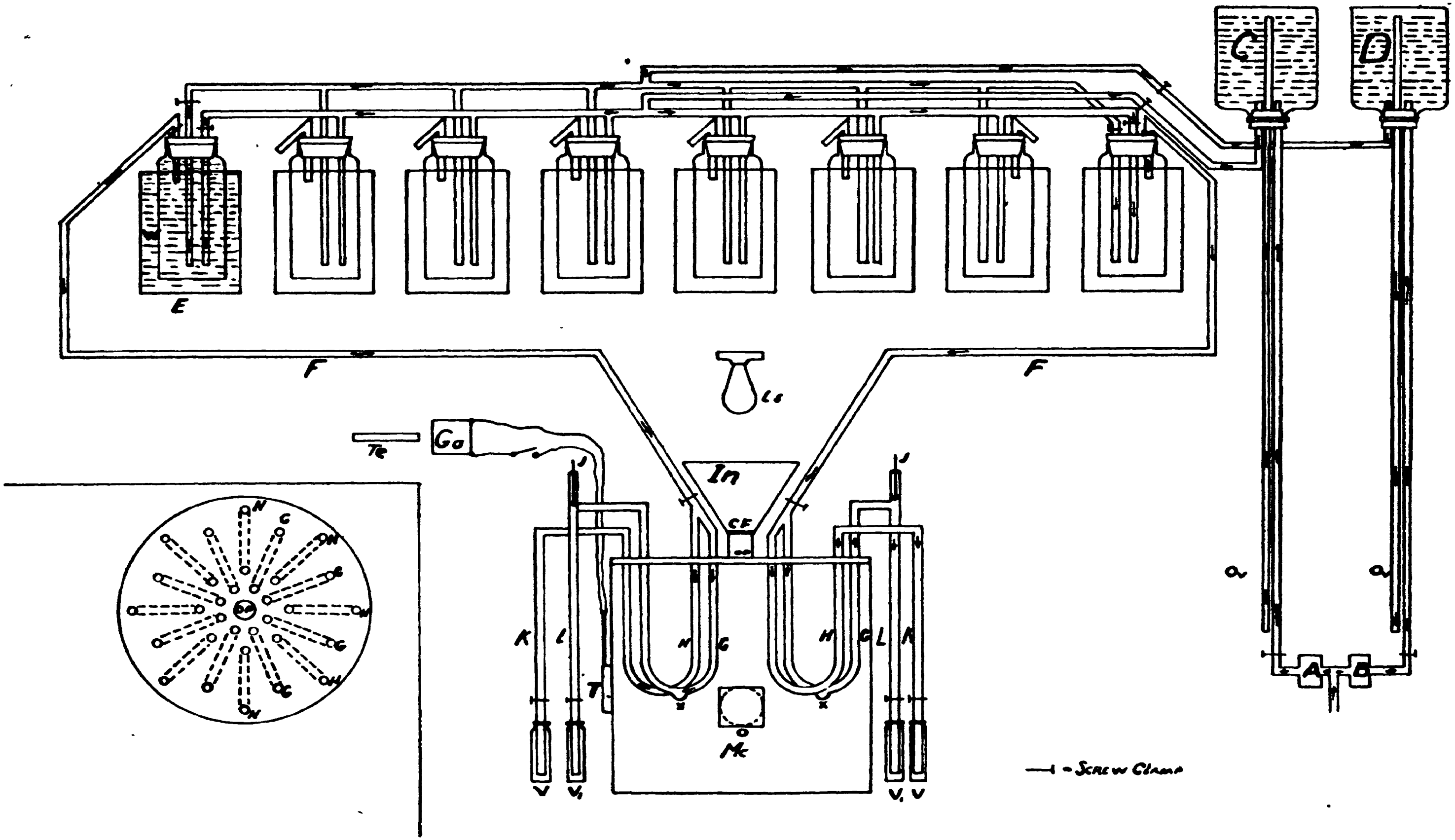

FIG. 2. Diagram of apparatus.

A, Refrigerator coils; *B*, Heater; *C*, Cold water pressure bottle; *D*, Hot water pressure bottle; *E*, Mixing bottle; *F*, Water supply to light apparatus; *G*, U-Tube containing eggs; *H*, U-Tube control; *Ga*, Galvanometer; *In*, Inverted reflector; *J*, Thermometer; *K*, Water from control tube; *L*, Water from egg tube; *Ls*, Light source; *Mc*, Mirrored glass container; *O*, Opening into container for observation; *OP*, Opening into container for light; *Ov*, Overflow tubes; *T*, Thermopile; *Te*, Telescope; *V* and V_1 Vials for oxygen samples; *W*, Water bath for mixing bottles; *CF*, Color filter. Inset shows pattern of arrangement of the U-tubes set into the top of the mirrored container.

surrounded by a water bath. The temperature of the water was controlled by regulating the rate of flow into the mixing bottles with screw clamps on the rubber tubing. This supplied running water at eight different temperatures which (usually) varied over a range of a degree and a half centigrade or less. Upon two occasions experiments were interrupted when external causes disturbed the entire water supply. The data collected from these latter experiments were discarded. The portion designed to contain the eggs consisted of a four liter Pyrex beaker from which the lip and flange had been cut. This was coated with silver on the outside and covered with quick-drying enamel. Two layers of silver were deposited by the technique described in the "Handbook of Physics and Chemistry." The top of the beaker was covered with a plate, likewise silvered, into which were set sixteen U-shaped tubes of eight mm. glass tubing. These U-tubes were radially arranged in pairs, one member of each pair having a slight depression blown into it at the bottom of the U. A circular opening, slightly over an inch in diameter, was cut in the center of the silvered plate. The U-tubes were cemented in so that the depression at the bottom was near the middle of the vertical height of the inside of the beaker. When completely sealed with glass cement and coated with enamel, this provided a light proof container holding a series of tubes through which water could be run, and which would reflect light coming in through the central opening (figure 2).

All eight sources of water, previously described, were run from above into this apparatus, a single source supplying both tubes of a pair—the control which never contained eggs and the tube with the depression into which eggs were placed. After flowing through the tubes, the water passed over thermometers to record temperature and then into vials set around the beaker and which supplied the water for the oxygen tests.

Light was furnished by a 1,000 Watt Edison Mazda Blue Photographic bulb, hung over the center of the mirrored beaker. An inverted conical metal lamp shade, whitened on the inside, served to protect the top of the mirrored container. The various wave lengths of light were secured by means of Corning glass filters placed and sealed across the opening into the egg container.

A copper-constantin thermopile with a quartz face was sealed in position outside the container, over an area from which the silver and enamel were removed. Likewise, low on one side, a circular opening for observation was made, an inch in diameter. This was sealed shut with light proof black paper, except for the short periods when examination of the eggs was necessary. These could be seen quite readily, lying in the depression in the U-tubes.

The apparent complexity of the apparatus was made necessary by the number of factors to be controlled, and was more apparent than real. Practice was required to get all the air out of the system, adjust the rates of flow and insert the eggs without disturbing the temperatures. Another occasional difficulty consisted in removing the tubing in which algae started to grow. The algal growths, fortunately, were few and the data which might have been affected were discarded.

Four of the beaker containers were prepared at the same time, and when during the course of the experiments, the silver showed signs of darkening, the container was replaced by another, previously unused.

Because the apparatus was constructed so that eight experiments could be run at one time, it was possible to collect eggs from a single set of snails, divide them up and place them at different temperatures under the same light conditions.

PROCEDURES

General.—The procedures followed during the course of the experiments using this apparatus, were standardized as much as possible to reduce the sources of error.

If the apparatus had been running satisfactorily, empty, at least six hours, a container of snails was removed from the cold-room, and the individuals placed two in a jar, the jars arranged in rows at room temperature.

Examination of the containers was made at regular intervals so that the eggs could be collected within, at the most, two hours after they were laid. After carefully scraping the masses from the glass, they were examined under a binocular microscope, to insure (1) that all eggs used were at the same stage of development, (2) that all eggs were alive and uninjured, and (3) that the exact number placed in the tubes was known. The eggs were then placed in the apparatus, the rate of flow and the temperature recorded and samples taken for oxygen analysis. The eggs were examined to make sure they could be satisfactorily seen in the tubes. The frequency of observations on the galvanometer deflection, oxygen consumption, rate of flow and temperature varied because it was found not feasible to attempt continuous recording through the night. The experimenter, however, was compelled to sleep in the laboratory, in order to make the tests as frequent as possible.

Temperature apparatus.—The constant temperature chambers, used in collecting some of the data discussed in a later portion of the paper consisted of incubators for temperatures above room temperature, sealed to prevent light entry, and incubators placed in the cold rooms for temperatures below room temperature. In such chambers eggs were placed in open, wide mouthed bottles and the length of time of development in hours recorded. Oxygen tests were not run as the water was not flowing and the size of the bottles prevented frequent sampling.

A series of glass stoppered, sealed bottles, was used, however, to check the total oxygen consumption per egg for the embryonic period. These were placed in the chambers discussed above.

The temperatures of the chambers varied little, but the recorded temperature for each experiment is the average hourly temperature throughout the entire developmental period. The same is true for the running water apparatus. In this case however the temperature variation was greater. The range of fluctuation was never greater than one and a half degrees.

Radiation measurements.—The amount of radiation available was kept constant by changing the position of the light suspended above the apparatus. The thermopile was equipped with a shutter, opened only when readings were made. A lapse of ten minutes following the raising of the shutter was sufficient to insure the maximum galvanometer deflection and to compensate for a lag in the thermopile. The total radiation of all wave lengths effecting the thermopile was kept between 2.85 and 2.95 cm. deflection, equivalent to an average of 1.31×10^{-3} gm. calories per square cm. per hour. When different filters were used, the light was adjusted to give the same energy reception by the thermopile. The thermopile was standardized and galvanometer calibrated by use of a U. S. Bureau of Standards lamp, No. C-252, set up according to instructions and checked.

The situation with regard to radiant energy during the experiments was, then, as follows:

1. All eggs within the container received the same amount of radiation as measured by the thermopile.
2. The radiation of the eggs was continuous and at the same intensity throughout each experiment. Equivalent intensities were used with each filter.

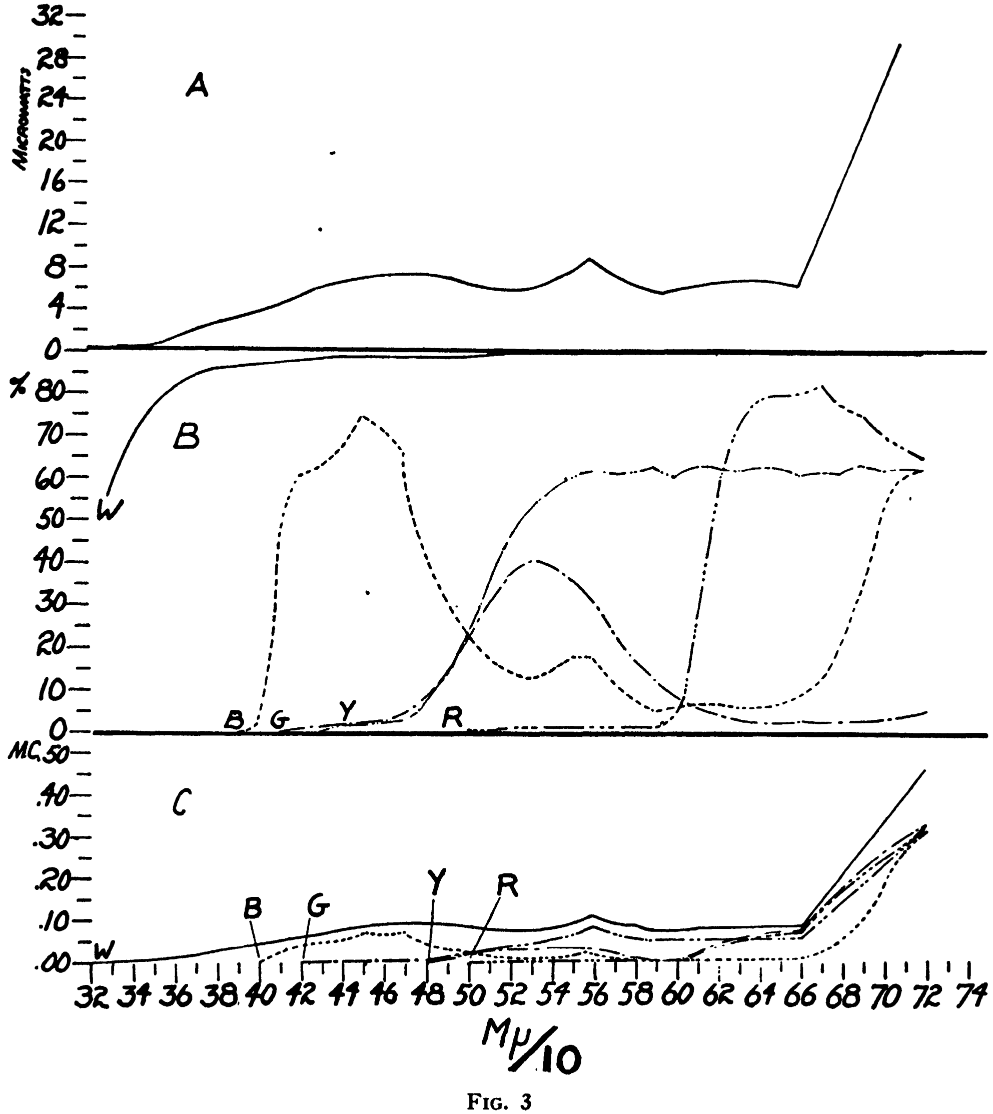

FIG. 3

A. Energy emission of the light source at 1 m. in microwatts per cm.^{2} per sec. per 50 Å. B. Per cent transmission of the filters used. C. Energy transmission of the filters used in millecalories per cm.^{2} per sec. W, White (Pyrex glass); B, blue; G, green; Y, yellow; R, red. Lower scale in mμ/10.

3. The differences in radiation were due to transmission by the filters of differential amounts of the energy emitted at each wave length by the light source. The total spectral energy per unit of time was constant.

In figure 3 the energy emission of the light source, the per cent transmission of each filter and the energy transmission of each filter are indicated.

Oxygen analysis.—A Micro-Winkler method of oxygen determination was used. The samples were collected in 35 cc. vials, each of which had a wax covered cork stopper fastened to it. The vials were left in place, continuously overflowing, from one sampling period to the next, to prevent the sample from taking up oxygen in filling. The collected samples were immediately stoppered and removed to the laboratory bench for the addition of reagents and analysis. A stock solution of .0025 N. sodium thiosulphate was used. This was standardized at each series of tests against a carefully made .0025 N. potassium dichromate solution. The burrettes used could be read to hundredths of a cubic centimeter. A 10 cc. sample from each vial was titrated and the cubic centimeters of sodium thiosulphate recorded as well as the standardization values. The difference in oxygen content between the control tube and egg tube was taken as the amount used by the eggs.

The rate of flow was recorded, using a stop watch, as the number of seconds required to fill a vial of known capacity. This is essential in making calculations on the amount of oxygen used per unit of time from a moving stream of water.

RATE OF DEVELOPMENT STUDIES

In table I are included the data from all rate of development experiments. The experiment numbers not preceded by a letter were in total darkness. Those designated as W, Y, G, R, and B represent white light, yellow, green, red and blue respectively. In each case the total eggs used, the number hatching, the average temperature (X), and the time in hours (Y), is shown. From these, rates ($1/Y$) were calculated and multiplied by 1000 for convenience in making graphs. The units per hour are derived by later calculations.

Total darkness.—The data are from two sources, (1) the constant temperature chambers, and (2) the experimental light apparatus which made possible oxygen tests.

At high and low temperatures both mortality and length of time to complete the embryonic development were high. As a result some eggs were placed at these extra-medial temperatures for a given length of time and then removed to complete development at a temperature in the medial range.

TABLE I. *Data on all rate of development experiments*

Experiment Number	Total Eggs	Eggs Hatching	Average Temperature (x)	Time in Hours (y)	Rate $1/y \times 1000$	Units per Hour
1a	7	7	22.30	250	4.000	11.93
1b	8	8	22.30	252	3.968	11.83
5a	7	7	22.08	260	3.846	11.47
5b	7	7	22.07	263.5	3.794	11.31
6a	6	6	29.50	153	6.535	19.49
6b	6	6	29.50	155	6.451	19.23
7a	7	7	21.77	248	4.032	12.02
7b	8	8	21.77	250	4.000	11.93
7c	4	4	21.77	249	4.016	11.97
7d	4	4	21.78	252	3.968	11.83
10a	8	8	25.28	196	5.102	15.21
10b	7	7	25.27	199	5.025	14.98
11a	7	7	29.04	157	6.369	18.99
11b	8	8	29.02	163	6.134	18.29
12a	5	5	29.01	158.5	6.349	18.93
12b	4	4	29.00	162.5	6.191	18.46
13a	5	5	25.21	201	4.975	14.83
13b	5	5	25.20	203	4.926	14.69
17a	7	7	19.93	343	2.915	8.69
17b	10	7	19.91	359	2.785	8.30
24a	5	5	22.87	252	3.968	11.83
24b	5	5	22.87	254	3.937	11.74
*27a	9	9	13.74	734	1.362	4.06
*27b	9	8	13.74	738	1.355	4.04
28a	8	8	14.70	666	1.501	4.48
28b	9	9	14.69	669	1.494	4.45
29a	11	11	18.78	318	3.144	9.37
29b	11	11	18.79	323	3.095	9.23
30a	5	5	19.90	311	3.215	9.58
30b	4	4	19.90	316	3.164	9.43
30c	5	5	19.90	310	3.225	9.62
30d	6	5	19.90	316	3.164	9.43
30e	7	7	19.90	311	3.215	9.59
30f	7	7	19.90	315	3.174	9.46
32a	6	6	19.96	323	3.095	9.23
32b	5	5	19.96	328	3.048	9.09
33a	6	6	22.84	241	4.149	12.37
33b	7	7	22.87	247	4.048	12.07
36a	6	6	20.05	313	3.194	9.52
36b	5	5	20.04	320	3.125	9.32
37a	15	12	24.39	209	4.784	14.26
37b	10	10	24.38	212	4.716	14.06
*31a	4	4	10.01	1502	.665	1.98
*31b	5	4	10.01	1510	.662	1.97
*26a	4	4	13.74	738	1.355	4.04
*26b	5	3	13.74	742	1.347	4.02
*34a	9	5	10.01	1500	.668	1.99
*34b	4	4	10.01	1517	.659	1.95
*54a	7	5	31.01	154	6.493	19.36
*54b	8	3	31.07	161	6.211	18.52
*55a	6	3	32.50	152	6.578	19.61
*55b	6	2	32.50	160	6.250	18.64

TABLE I (*Continued*)

Experiment Number	Total Eggs	Eggs Hatching	Average Temperature (x)	Time in Hours (y)	Rate $1/y \times 1000$	Units per Hour
*56a	4	2	33.65	172	5.813	17.33
*56b	4	1	33.67	175	5.714	17.04
*59	6	3	35.00	196	5.102	15.21
61b	4	4	25.17	191	5.235	15.61
62a	5	5	25.17	193	5.181	15.45
63b	8	8	19.74	321	3.115	9.29
64a	7	7	25.19	196	5.102	15.21
65a	5	5	19.74	322	3.105	9.26
65b	6	6	18.91	347	2.881	8.59
66b	4	4	18.91	347	2.881	8.59
T2	63	63	20.79	288	3.472	10.35
T6	57	57	20.76	286	3.496	10.42
T12	65	65	21.20	268	3.731	11.12
T10	90	90	26.44	185	5.405	16.12
*14a	12	12	8.00	100	.388	1.16
*14b	11	11	8.00	100	.340	1.01
*15a	7	6	9.00	100	.491	1.46
*15b	6	6	9.00	100	.539	1.61
*16a	4	4	8.00	100	.407	1.21
*16b	6	6	8.00	100	.324	0.97
*19a	4	4	10.00	100	.748	2.23
*19b	4	4	10.00	100	.611	1.82
*20a	10	10	10.00	105	.834	2.49
*20b	9	9	10.00	105	.794	2.37
*21a	7	7	9.00	105	.319	0.95
*21b	7	7	9.00	105	.231	0.69
*38a	8	8	10.00	200	.676	2.02
*38b	8	8	10.00	200	.654	1.95
*40a	15	15	10.00	239	.683	2.04
*40b	16	16	10.00	239	.663	1.98
*44	8	8	10.02	568	.707	2.11
*57a	4	2	34.50	100	5.461	16.28
*57b	4	2	34.50	100	5.413	16.14
*60a	6	4	36.00	100	3.698	11.03
*60b	6	3	36.00	100	3.648	10.88
*60c	8	3	36.00	200	3.718	11.09
*60d	8	2	36.00	200	3.701	11.04
W14	124	112	20.48	326	3.067	9.16
W12	114	99	21.75	313	3.195	9.54
W16	53	46	22.35	281	3.559	10.63
Y2	41	37	23.14	290	3.448	13.76
Y4	27	27	24.45	266	3.759	15.00
Y8	35	33	22.20	315	3.175	12.67
Y10	46	44	24.60	267	3.745	14.95
Y12	49	44	24.08	274	3.650	14.57
Y16	39	38	24.46	269	3.717	14.83
G2	68	53	20.37	499	2.004	11.10
G6	69	56	21.82	445	2.247	12.44
G8	95	85	23.64	391	2.558	14.16
R2	51	47	20.06	331	3.021	9.99
R4	46	43	23.83	250	4.000	13.23
R6	40	36	24.85	221	4.525	14.97
R10	47	42	26.78	200	5.000	16.54
R12	45	39	27.36	193	5.181	17.14
R14	52	47	25.83	209	4.785	15.83
R16	45	42	22.04	286	3.497	11.57
B6	42	39	23.86	315	3.175	14.63
B10	51	47	26.78	266	3.759	17.32
B12	45	42	27.56	253	3.953	18.21
B14	48	46	26.22	280	3.571	16.45
B2	59	54	16.67	102	1.677	7.73
B4	55	51	18.75	102	2.148	9.90
CD1	26	22	25.44	187	5.348	15.95
A	5	5	13.63	796	1.256	3.75
*C	5	5	32.50	159	6.289	18.75
D	5	5	19.11	333	3.003	8.95
E	5	5	24.92	202	4.950	14.76
G4	54	38	21.02	498	2.008	11.12

* = above or below medial temperatures.

In table II are listed all experiments in total darkness which were completed at a single temperature including incubator and apparatus experiments. The latter are designated with a prefix T. Following Von Oettingen's method of calculating *alpha*, from a graph of the reciprocals of the time in hours *alpha* values were selected by trial and error, and substituted in the equation $(x - \alpha)y = K$, in each experiment. The weighted mean K was then calculated and the mean deviation from it in the individual experiments computed. The *alpha* value giving the smallest deviation was 10.32° C. The mean constant (K) was 2981.7.

The constant and *alpha* values for the apparatus and incubator experiments, which differed mainly in the presence and absence of flowing water, were calculated separately. When tested for variance (Snedecor, 1934) the differences were found not to be significant and the values $K = 2981.7$ and $\alpha = 10.32°$ C. represent the combined data. Inspection showed that the medial temperature range (the straight line portion of the curve), was from 14.5° C. to 29° C The standard deviation of *alpha* was

.339° C. The standard deviation of the constant (K) was 101.02 units.

In table III are shown the results of calculating rate of development and units per hour at the low and high temperatures to which these eggs were exposed for a definite time before being placed at medial temperatures to complete development. Figure 4 shows both rates and units per hour for all total darkness data. This curve served as a basis for comparison with the results of the light-temperature experiments.

TABLE II. *Constant darkness. Eggs at a single temperature*

Exp. No.	Eggs Hatched	Average Temperature	K (α = 10.32)	d_1 (K = 2981.7)	α (K = 2981.7)	d_2 (α = 10.32)
1a	7	22.30	2995.0	13.3	10.37	.05
1b	8	22.30	3019.0	37.3	10.47	.15
5a	7	22.08	3057.6	75.9	10.61	.29
5b	7	22.07	3096.1	114.4	10.75	.43
6a	6	29.50	2934.5	47.2	10.01	.31
6b	6	29.50	2972.9	8.8	10.26	.06
7a	7	21.77	2839.6	142.1	9.75	.57
7b	8	21.77	2862.5	119.2	9.84	.48
7c	4	21.77	2851.1	130.6	9.80	.52
7d	4	21.78	2887.9	93.8	9.95	.37
10a	8	25.28	2932.2	49.5	10.07	.25
10b	7	25.27	2975.1	6.6	10.29	.03
11a	7	29.04	2939.0	42.7	10.05	.27
11b	8	29.02	3048.1	66.4	10.73	.41
12a	5	29.01	2962.4	19.3	10.20	.12
12b	4	29.00	3035.5	53.8	10.65	.33
13a	5	25.21	2992.9	11.2	10.38	.06
13b	5	25.20	3020.6	38.9	10.51	.19
17a	7	19.93	3296.2	314.5	11.24	.92
17b	7	19.91	3442.8	461.1	11.60	1.28
24a	5	22.87	3162.6	180.9	11.04	.72
24b	5	22.87	3187.7	206.0	11.13	.81
*27a	9	13.74	2510.3			
*27b	8	13.74	2524.0			
28a	8	14.70	2917.1	64.6	10.22	.10
28b	9	14.69	2923.5	58.2	10.23	.09
29a	11	18.78	2690.3	291.4	9.40	.92
29b	11	18.79	2735.8	245.9	9.56	.76
30a	5	19.90	2979.4	2.3	10.31	.01
30b	4	19.90	3027.3	45.6	10.46	.14
30c	5	19.90	2969.8	11.9	10.28	.04
30d	5	19.90	3027.3	45.6	10.46	.14
30e	7	19.90	2979.4	2.3	10.31	.01
30f	7	19.90	3017.7	36.0	10.43	.11
32a	6	19.96	3113.7	132.0	10.73	.41
32b	5	19.96	3161.9	180.2	10.87	.55
33a	6	22.84	3017.3	35.6	10.47	.15
33b	7	22.87	3099.9	18.2	10.80	.48
36a	6	20.05	3045.5	63.8	10.52	.20
36b	5	20.04	3110.4	128.7	10.72	.40
37a′	12	24.39	2940.6	41.1	10.12	0.20
37b	10	24.38	2980.7	1.0	10.23	0.00
*31a	4	10.01				
*31b	4	10.01				
*26a	4	13.74	2524.0			
*26b	3	13.74	2537.6			
*34a	5	10.01				
*34b	4	10.01				
*54a	5	31.01	3186.3			
*54b	3	31.07	3340.8			
*55a	3	32.50	3371.4			
*55b	2	32.50	3548.8			
*56a	2	33.65	4012.8			
*56b	1	33.67	4086.3			
*59	3	35.00	4837.3			
61b	4	25.17	2836.4	145.3	9.56	0.76
62a	5	25.17	2866.1	115.6	9.72	0.60
63b	8	19.74	3023.8	42.1	10.45	0.13
64a	7	25.19	2914.5	67.2	9.98	0.34
65a	5	19.74	3033.2	51.5	10.48	0.16
65b	6	18.91	2980.7	1.0	10.32	0.00
66a	4	18.91	2980.7	1.0	10.32	0.00
T2	63	20.79	3015.4	33.7	10.44	0.12
T6	57	20.76	2985.8	4.1	10.33	0.01
T12	65	21.20	2915.8	65.9	10.07	0.25
T10	90	26.44	2982.2	.5	10.32	0.00

* = above or below medial temperatures.
$K = 2981.7 \pm 4.19$.
$\sigma_K = 101.02$.
$\alpha = 10.32 \pm .014$.
$\sigma_\alpha = .339$.

The best graphic fit to the data below 14.5° C. was found to be another straight line, having a different slope. The formula for this line (data graphed as rate, $1000/y$, against temperature, x), is $y = ax - b$, when $a = .178$ and $b = 1.099$. When graphed to read in terms of developmental units, multiplying by the constant gives the formula $y = ax - b$, when $a = .5308$ and $b = 3.277$. This line intersects the temperature axis at approximately 6.2° C. (Exactly 6.174° C.) The true threshold

TABLE III. *Constant darkness. Eggs at two temperatures*

No.	No. of Eggs	Medial Temp. X_2	$X_2 - \alpha$ $\alpha = 10.32$	Hours Y_2	Units $Y_2(X_2 - \alpha)$	d. $K = 2981.7$	Hours Y_2	Units per hr. $\frac{\text{Diff}}{Y_1}$	Extra-medial Temp. (X_1)	Rate × 1000 at X_1
14a	12	24.65	14.33	200	2866	115.7	100	1.157	8.0	.3880
14b	11	24.65	14.33	201	2880.3	101.4	100	1.014	8.0	.340
15a	6	24.64	14.32	198	2835.4	146.3	100	1.463	9.0	.491
15b	6	24.64	14.32	197	2821.0	160.7	100	1.607	9.0	.539
16a	5	22.81	12.49	229	2860.2	121.5	100	1.215	8.0	.407
16b	5	22.81	12.49	231	2885.2	96.5	100	.965	8.0	.3236
19a	4	24.54	14.22	194	2758.7	223.0	100	2.230	10.0	.7478
19b	4	24.53	14.21	197	2799.4	182.3	100	1.823	10.0	.6113
20a	10	22.80	12.48	218	2720.6	261.1	105	2.487	10.0	.8340
20b	9	22.80	12.48	219	2733.1	248.6	105	2.368	10.0	.7941
21a	7	22.85	12.53	230	2881.9	99.8	105	.950	9.0	.3186
21b	7	22.86	12.54	232	2909.3	72.4	105	.690	9.0	.2314
38a	8	23.82	13.50	191	2578.5	403.2	200	2.016	10.0	.6761
38b	8	23.82	13.50	192	2592.0	389.7	200	1.949	10.0	.6536
40a	15	24.03	13.71	182	2495.2	486.5	239	2.036	10.0	.6828
40b	16	24.03	13.71	183	2508.9	472.8	239	1.978	10.0	.6633
44	8	24.95	14.63	122	1784.9	1196.8	568	2.107	10.02	.7066
57a	2	24.87	14.55	93	1353.2	1628.5	100	16.285	34.50	5.461
57b	2	24.87	14.55	94	1367.7	1614.0	100	16.140	34.50	5.413
60a	4	25.00	14.68	128	1879.0	1102.7	100	11.027	36.00	3.698
60b	3	25.00	14.68	129	1893.7	1088.0	100	10.88	36.00	3.648
60c	3	20.00	9.68	79	764.7	2217.0	200	11.085	36.00	3.718
60d	2	20.00	9.68	80	774.4	2207.3	200	11.036	36.00	3.701

then is in the vicinity of 6.2° C. and differs from the *alpha* point by 4.12 degrees.

No single curve could be found to describe the data on rate between 20° C. and 36° C. Between 32° and 35° a satisfactory curve was fitted having the formula $y = ae^{-rt}$ when $a = 121.64$, $r = .0904$, and $e =$ the base of Naperian logarithms. The raised curve, reading in developmental units has the same formula, with $a = 363.73$ and $r = .0904$. The line from 35° to 36° C. is a straight line connecting the two points.

White light and colored light.—The same procedures, using Von Oettingen's method of calculating *alpha* and the constant, were applied to the data for constant white, yellow, green, red and blue light. Analysis of variance indicated that when treated as a series the differences in K values for all radiation conditions are significant. When analyzed in groups of two, however, the constants for total darkness and for white light did not differ significantly. All other combinations, however did.

The question arose as to whether the differences in rates of development were due to differences in temperature within the egg masses, caused by absorbtion of radiant energy.

The galvanometer was standardized with a copper-constantin thermocouple and a deflection of .1 cm. for every .0458° C. difference in temperature recorded. Eggs were then exposed to the various light conditions under the intensity used in experiments with the thermocouple inserted into the jelly mass. A control run in total darkness showed no heating effect whatever. The temperatures shown in table IV indicate the amount of heating due to absorption of radiant energy. This temperature correction was applied to all colored light experiments and *alpha* values.

The *alpha* values, corrected, differed from the *alpha* of the dark curve by the

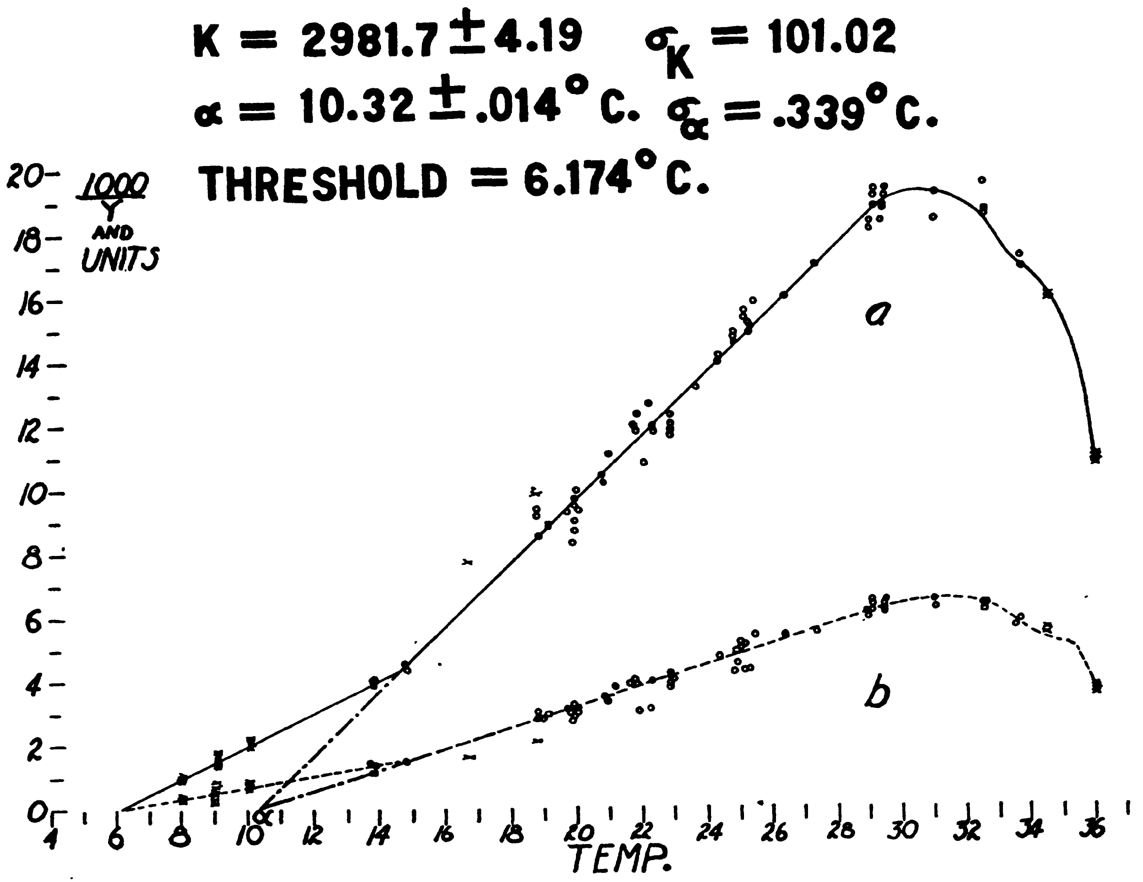

FIG. 4. Temperature-velocity curve for darkness.

a, Velocity in units; *b*, velocity as 1000/*y*. ○ = Experiments at a single temperature, in incubators. ● = Experiments at a single temperature in light apparatus. *x* = Experiments at two temperatures. □ = Sealed bottle experiments. $K = 2981.7 \pm 4.19$. $\sigma_K = 101.02$, $\alpha = 10.32 \pm .014°$ C., $\sigma_\alpha = .339°$ C. Threshold = 6.174° C.

TABLE IV. *Temperature increase in egg mass* (Thermocouple)

Galvanometer deflection. .1 cm. = .0458° C.

Light Filter	Radiation Intensity (Thermopile; Deflection in cm.)	Thermocouple Deflection (in cm.)	Temperature Increase
Dark	0	0	0
White	2.85	.15	.069
Yellow	2.85	.25	.115
Green	2.90	.20	.092
Red	2.92	.57	.261
Blue	2.95	.03	.014

various multiples of the standard deviation shown in the last column of table V.

The chances that these *alpha* values are not significantly different from the dark *alpha* are:

1 in 17,000 for white light
1 in 100 for blue light
1 in 36 for green light
1 in 22 for yellow light
1 in 1 for red light

Whereas the constants for darkness and white light were not significantly different, while all others were, the *alpha* values of darkness and white light show the greatest significant difference and the darkness-red difference is definitely not significant.

Figure 5 shows the various temperature-velocity relationships in colored light. Figure 5, A shows the velocity curves for darkness and white light plotted on the same scales and indicates the similarity in rate.

The following two lists show the relative positions of the *alpha* values and the constants:

Thresholds, low to high:	Blue	9.47° C.
	Green	9.57° C.
	Yellow	9.65° C.
	Dark	10.32° C.
	Red	10.48° C.
	White	11.80° C.
Constants, low to high	Dark	2981.7
	White	2985.4
	Red	3308.2
	Yellow	3990.9
	Blue	4607.1
	Green	5536.7

SURVIVAL

Mortality and temperature.—A study of the per cent mortality over various temperature ranges of the velocity curve for darkness was made. The temperature scale was divided into six portions, each, except the last, including the data grouped over a five degree range. In the experiments from which the data were compiled, no egg masses which failed to produce live, hatched young were considered. The mortality for all the experiments was 7.04 per cent. The data are shown graphically in Figure 6, B. That portion of the temperature scale which includes the point at which the velocity-temperature relationship changes (10.1° to 15°), appears to be a region of great susceptibility, as evidenced by the high mortality of 10.81 per cent.

Mortality and colored light.—The effects of radiation in these experiments upon the viability of the eggs was considered

TABLE V. *Temperature corrections for alpha*

Light Filter	α	Correction for temp. of Egg Mass (degrees C.)	Corrected α	Standard Deviation of α's	d. Difference from $\alpha = 10.32$	$\frac{d}{.339}$
Dark	10.32	0	10.32 ± .014	.339	0	0
Blue	9.46	.014	9.47 ± .015	.20	.85	2.51
Green	9.48	.092	9.57 ± .013	.203	.75	2.21
Yellow	9.53	.115	9.65 ± .006	.095	.67	1.98
Red	10.22	.261	10.48 ± .014	.235	.16	.47
White	11.73	.069	11.80 ± .025	.403	1.48	4.37

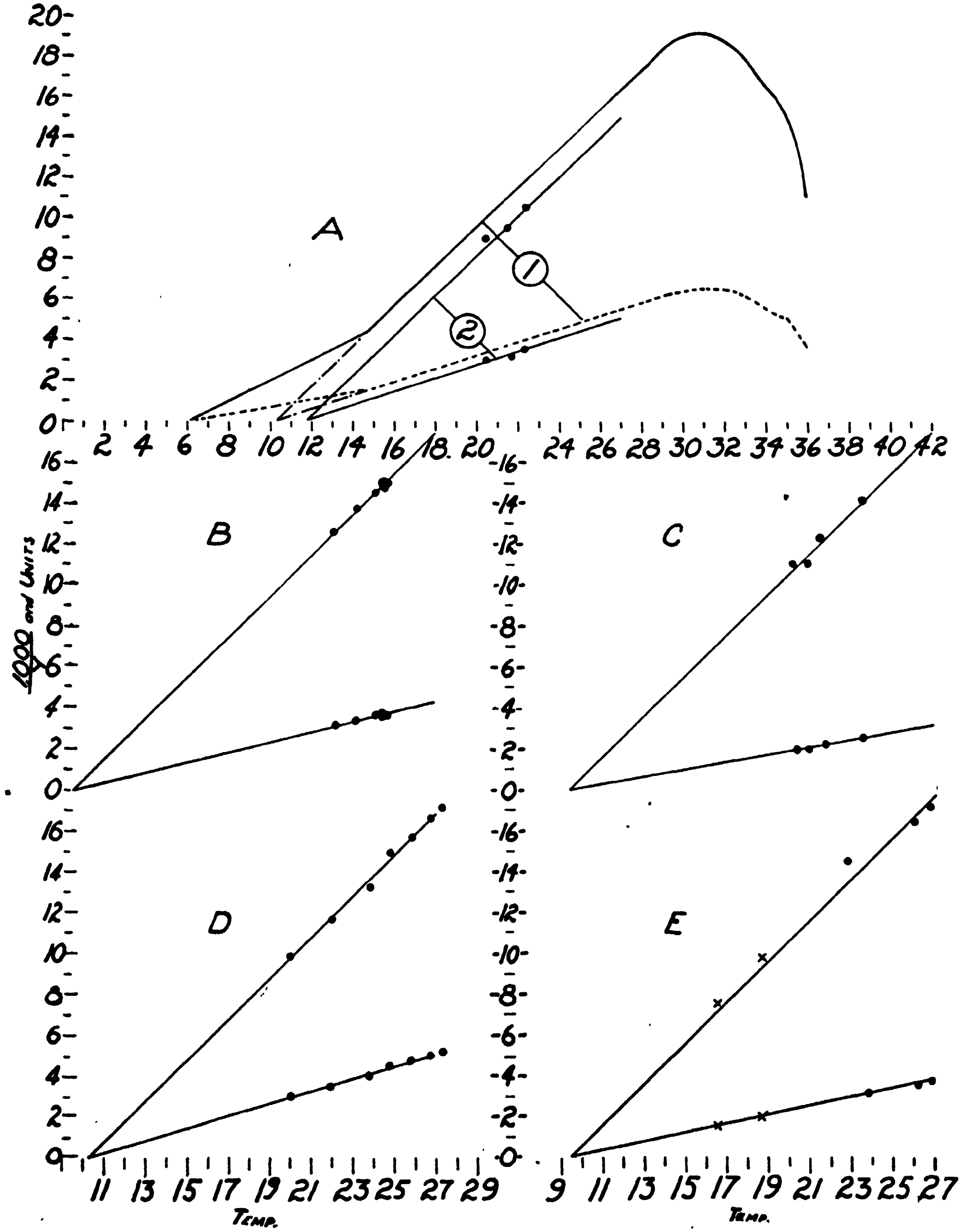

FIG. 5. Temperature-velocity curves for various light conditions.

A. 1. Repetition of figure 4. 2. Velocity curve for white light. $K = 2985.38 \pm 8.0$, $\sigma_K = 128.31$, corrected $\alpha = 11.80 \pm .025°$ C., $\sigma_\alpha = .403°$ C. B. Velocity curve for yellow light. $K = 3990.88 \pm 1.78$, $\sigma_K = 26.56$, corrected $\alpha = 9.65 \pm .006°$ C., $\sigma_\alpha = .095°$ C. C. Velocity curve for green light. $K = 5536.69 \pm 6.61$, $\sigma_K = 100.7$, corrected $\alpha = 9.57 \pm .013°$ C.; $\sigma_\alpha = .203°$ C. D. Velocity curve for red light. $K = 3308.18 \pm 3.42$; $\sigma_K = 58.88$; corrected $\alpha = 10.48 \pm .014°$ C.; $\sigma_\alpha = .235°$ C. E. Velocity curve for blue light. $K = 4607.12 \pm 4.33$; $\sigma_K = 57.11$; corrected $\alpha = 9.47 \pm .015°$ C.; $\sigma_\alpha = .20°$ C. ● = Experiments at a single temperature. X = Experiments at two temperatures. The lower line in each case is velocity as $1000/y$. The upper line is velocity in units.

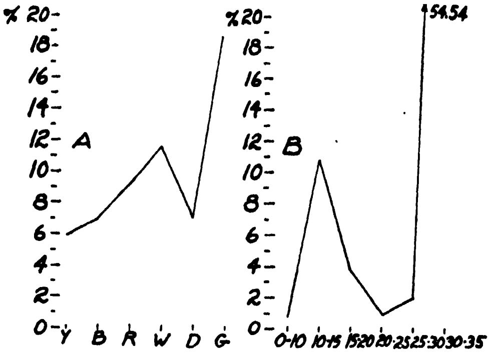

Fig. 6

A. Mortality in per cent and color of light.
B. Mortality in per cent and temperature.

to be an important part of the general problem of the light effect. The entire data for each kind of light were grouped, irrespective of temperature. Only in darkness and in green light did entire egg masses fail to hatch. The per cent mortality could then be calculated to include these data, or without them. For the graph of Figure 6, A, only those egg masses from which some or all of the embryos hatched were counted. Both white and green light produced a per cent mortality greater than that of the average for all experiments which was 9.26 per cent. If the masses which failed entirely to hatch are included the results are somewhat different, in that the highest mortalities are then under green light and in darkness. The more reliable analysis of the two is probably the first, because the number of individuals included in the dark experiments is several times greater than in any of the others; undoubtedly if more experiments had been run under the other light conditions some entire egg masses would have failed to hatch.

Results of Oxygen Consumption Studies

Calculations.—The general technique of the oxygen consumption tests has been discussed earlier in this report, but more detail is appropriate as a preliminary to the discussion of results. The raw data consisted of the following:

1. The number of seconds to fill a vial of known capacity with the flowing water;
2. The number of cubic centimeters of sodium thiosulfate required in titration of a 10 cc. sample from both the control and the tube containing eggs;
3. The number of cubic centimeters of .0025 N. potassium dichromate necessary to standardize 10 cc.'s of sodium thiosulfate solution;
4. The number of eggs in the tube;
5. The temperature.

From these figures the number of cubic centimeters of oxygen per liter in the control sample was calculated (see Stand. Meth. Water Analysis). The process was repeated for the sample from the tube containing eggs. The difference represents the amount of oxygen used per liter of water. Then by calculating the rate of flow of the water in liters per hour, the oxygen consumption per hour per egg can be derived. At the time the tests were made the date and time were recorded so that the number of hours after laying could be used in following changes in oxygen utilization. The quantity of oxygen was so small that for convenience the values were multiplied by 1,000.

The data included in table VI were selected from the slightly larger quantity of information collected because they seemed to be typical of the oxygen consumption under various light conditions.

Temperature and oxygen consumption.—The amount of oxygen used by the embryos per hour did not show a regular rate of increase throughout the developmental period. Instead, as is seen in figure 7, a great deal of fluctuation occurred. Comparison of two separate experiments at the same temperature and in the same light condition indicates similar modes, or peaks of consumption rate, and that approximately the same modes occur, with a few exceptions, in all experiments. The two top curves of figure 7, A and B, show the rate of utilization in darkness at an average temperature of 20.8° C. Curve *C* is from eggs in darkness at 26.4° C. The more rapid development at the higher temperature is apparent, as is also the fact that similar modes occur, but closer together. The lower curve, *D*, should be compared with A and B. The data are from eggs in white light at approximately the same temperature as the two darkness curves, 20.6° C. The failure to coincide in certain portions may be due to errors in sampling, too long a period elapsing between tests.

Light and oxygen consumption.—Comparison of the curves of consumption rate in figure 8 shows the same similarity in general form for all light conditions except green. The top curve, *A*, is a repetition of curve *D*, figure 7. These are also at approximately the same temperature, with the exception of the white light curve.

Total oxygen used.—Comparisons of

TABLE VI

O_2 = cc. × 1,000. T = No. of hours after laying. Oxygen consumed per egg per hr. in cc. × 1,000. *X* = Temperature in centigrade

		Dark				White		Yellow		Red		Blue		Green	
Tube 5–6		Tube 1–2		Tube 9–10		Tube 13–14		Tube 1–2		Tube 3–4		Tube 5–6		Tube 7–8	
X = 20.8°		*X* = 20.8°		*X* = 26.4°		*X* = 20.57°		*X* = 23.26°		*X* = 24.09°		*X* = 23.87°		*X* = 23.73°	
T	O_2	T	O_2	T	O_2	T	O_2	T	O_2	T	O_2	T	O_2	T	O_2
5	6.0	10	6.3	2	7.8	14	6.7	2	2.1	3	5.3	2	4.8	5	3.0
11	7.3	18	4.4	6	9.9	19	1.4	13	1.5	8	6.3	5	5.5	10	3.8
15	1.6	24	6.4	9	6.7	42	8.1	18	6.0	11	5.9	9	5.6	16	1.5
24	3.4	29	1.8	11	2.9	50	6.0	24	1.1	15	5.2	15	6.1	20	1.0
29	3.1	32	7.8	16	5.3	55	3.7	35	5.0	19	5.0	26	5.0	30	1.7
32	8.6	37	12.2	25	11.2	64	2.2	38	6.6	29	3.0	30	4.1	35	1.7
36	8.3	51	2.7	30	4.6	68	3.5	40	8.3	36	10.4	35	4.2	44	3.9
48	2.8	55	1.8	35	5.0	71	5.0	44	2.1	42	3.4	38	3.6	52	4.0
53	2.4	57	2.5	42	2.9	80	2.7	50	4.6	52	4.0	44	6.0	58	2.5
57	3.7	65	7.5	55	2.6	83	3.4	62	3.4	55	6.5	52	8.5	61	2.2
62	7.2	78	1.3	60	2.0	86	0.7	65	5.4	58	6.0	62	3.0	66	1.4
65	2.0	84	1 9	75	15.1	88	0.9	70	3.3	66	1.4	66	3.7	78	1.9
71	4.3	88	1.0	79	1.7	90	1.0	76	3.8	68	1.9	78	5.7	86	3.7
73	0.7	97	1.7	82	11.5	107	0.8	84	1.4	77	1.5	85	4.1	101	2.2
76	1.0	102	2.4	84	4.2	138	7.4	88	2.2	83	1.7	89	1.5	106	0.6
79	1.7	105	0.8	89	5.8	140	9.0	92	0.8	86	1.8	98	1.8	109	1.1
83	2.3	109	2.0	98	4.5	184	3.0	97	1.0	91	2.1	103	1.6	112	0.7
85	0.6	121	9.1	101	7.8	194	2.5	107	2.0	99	8.1	106	1.2	115	1.2
96	1.3	126	2.2	106	4.3	201	2.7	114	2.4	101	8.9	112	1.4	126	0.4
103	2.1	130	9.0	110	7.1	205	4.5	118	4.5	104	5.0	122	1.8	131	0.6
105	1.1	135	2.0	114	3.5	209	1.8	122	7.9	109	10.1	126	1.9	136	0.8
108	1.8	138	5.2	122	2.7	211	2.0	133	2.0	113	3.0	138	6.0	141	0.9
109	1.8	144	2.8	124	3.1	221	2.9	135	8.1	124	2.6	145	5.6	149	1.0
121	10.8	146	2.5	127	4.0	227	1.8	138	5.6	126	2.5	149	8.8	154	1.1
126	1.1	149	2.5	130	2.6	234	0.4	144	4.7	129	4.1	154	6.5	160	4.6
130	9.2	152	2.7	133	0.8	243	2.1	147	3.7	132	3.1	157	3.0	163	5.0
135	2.9	156	5.8	136	2.2	249	0.5	155	3.1	137	3.3	162	2.9	174	6.6
138	4.8	158	3.5	144	3.5	253	0.8	161	3.6	139	2.8	170	2.2	176	4.1
144	3.2	169	2.5	147	3.0	257	1.5	164	5.2	141	2.5	180	2.4	178	4.5
146	3.3	176	4.6	151	1.6	268	2.6	170	2.7	151	5.5	184	3.5	182	5.5
149	3.2	178	1.5	157	3.0	274	2.0	180	4.1	156	2.2	196	2.5	186	6.0
152	3.1	181	1.2	159	2.6	282	1.1	187	0.8	158	2.8	203	3.2	196	1.9
156	5.4	182	1.6	169	2.4	290	2.1	190	2.5	162	3.5	207	4.0	199	2.7

Table VI (*Continued*)

Dark						White		Yellow		Red		Blue		Green	
Tube 5–6		Tube 1–2		Tube 9–10		Tube 13–14		Tube 1–2		Tube 3–4		Tube 5–6		Tube 7–8	
$X = 20.8°$		$X = 20.8°$		$X = 26.4°$		$X = 20.57°$		$X = 23.26°$		$X = 24.09°$		$X = 23.87°$		$X = 23.73°$	
T	O_2	T	O_2	T	O_2	T	O_2	T	O_2	T	O_2	T	O_2	T	O_2
158	3.0	194	3.1	172	6.6	296	1.7	193	2.9	171	1.0	211	4.6	205	1.6
169	2.6	199	2.2	174	3.2	299	4.0	205	1.0	174	0.8	219	1.7	211	1.5
173	3.0	203	1.6	177	8.7	307	3.4	207	1.0	178	1.6	223	2.2	223	2.2
176	4.9	208	2.9	180	10.1	320	6.5	209	1.8	184	4.3	229	2.5	227	1.4
178	2.0	211	1.3	183	13.5	327	11.5	216	1.7	186	3.0	233	2.6	232	1.3
192	3.3	217	1.0	185	15.5			227	1.9	196	1.5	244	2.3	235	1.1
196	1.6	219	1.1					230	2.9	199	1.6	248	3.5	245	1.5
199	2.2	222	2.4					233	2.7	203	1.0	253	2.4	247	2.5
201	0.5	225	3.7					238	2.6	204	1.0	256	2.0	250	2.6
206	2.7	229	2.7					243	1.9	209	1.9	258	1.4	254	0.7
215	0.5	231	2.0					252	1.5	219	1.7	266	0.8	258	1.5
220	1.6	242	1.5					254	1.9	221	1.6	268	1.0	268	1.5
225	2.8	246	0.9					258	2.0	225	1.6	275	1.8	273	1.4
232	2.5	249	2.6					264	1.9	233	3.6	279	1.5	278	1.2
245	1.1	251	1.9					268	1.8	244	3.1	281	1.8	283	1.4
250	2.1	265	1.2					276	4.0	247	9.5	291	1.7	285	0.9
265	1.7	269	2.6					282	3.0	249	11.0	294	2.9	294	1.1
269	4.5	272	1.8					286	7.3	251	12.9	296	4.1	300	0.9
272	2.3	274	2.3					288	8.7			302	3.1	306	1.0
274	3.0	279	5.5					291	10.5			307	2.1	318	1.4
279	6.1	288	12.5									314	7.5	320	1.6
288	11.9											316	10.0	322	1.6
														325	1.4
														328	1.4
														340	1.2
														345	0.8
														351	0.7
														355	0.8
														357	1.1
														365	1.0
														371	0.9
														373	0.9
														377	0.8
														380	1.0
														390	1.5
														393	1.9

metabolic rate as indicated by the rate of oxygen consumption are based upon the assumption that the total amount of metabolism necessary to complete any given stage of growth or development is approximately a constant, irrespective of temperature. Higher temperatures produce a faster rate, but the same total amount of energy is used. Evidence that this is so has been collected by a number of workers, including Krogh ('14) and Northrup ('26). Most of this was based upon carbon dioxide production rather than oxygen consumption. What is true for one however will be true of the other, especially during embryonic development when food supply is constant. The area under each curve was taken as an approximation of the total oxygen consumed. The results of this tabulation are as follows:

Dark, at 20.8° C. = 1.0570 cc. of O_2 per egg
Dark, at 20.8° C. = .9616 cc. of O_2 per egg
Dark, at 26.4° C. = 1.0561 cc. of O_2 per egg
Green, at 23.7° C. = .7630 cc. of O_2 per egg
Red, at 24.1° C. = .8982 cc. of O_2 per egg
Yellw, at 23.3° C. = .9058 cc. of O_2 per egg
Blue, at 23.9° C. = 1.0907 cc. of O_2 per egg
White, at 20.6° C. = 1.1946 cc. of O_2 per egg

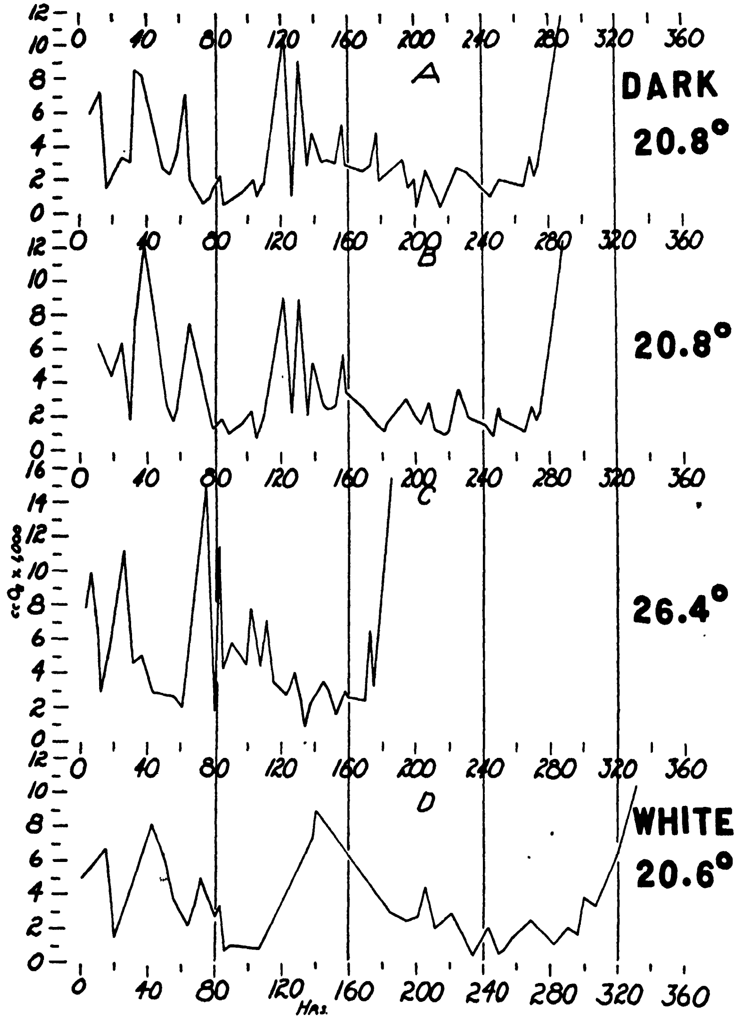

FIG. 7. Oxygen consumption and development.
A. Darkness, 20.8° C. B. Darkness, 20.8° C. C. Darkness, 26.4° C. D. White light, 20.6° C.

The mean O_2 consumption per egg was 1.0070 ± .00621 cc. The standard deviation of these data is .14233 ± .00439 cc. The differences from the mean are small enough multiples of the standard deviation (less than twice) so that they are probably not significant. The most nearly significantly different value is the total for green.

To serve as a check on this portion of the experiment, a series of glass stoppered bottles, from one to three liters content, was filled with water, the dissolved oxygen measured, five eggs placed in each bottle, paraffin oil placed over the top and the glass stoppers inserted. The bottles were then placed at different temperatures in darkness. When the eggs within the bottles hatched the oxygen content was again determined and the difference taken as the amount consumed by the eggs. The mean total oxygen consumed per egg was 1.0945 cc. This checks within the limits of experimental error with the mean totals as determined by the graphic method. Variation in volume produced no significant variations in totals.

The experimental error in the oxygen measurement, dependent upon the limits of accuracy of measurement, and upon the number of eggs in an experiment, does not exceed ± .0005 cc. of oxygen per egg. The number of eggs per exeperimnt varied from 37 to 112.

Discussion.—One interesting feature of the temperature-velocity curve is the fact that the lower portion bears a straight line relationship to the temperature axis. Most of the curves reported in the literature show a concave region between the true threshold (6.2° C.) and the point of intersection with the straight line representing the rate at medial temperatures (14.5° C.). There is then offered the possibility of using this lower

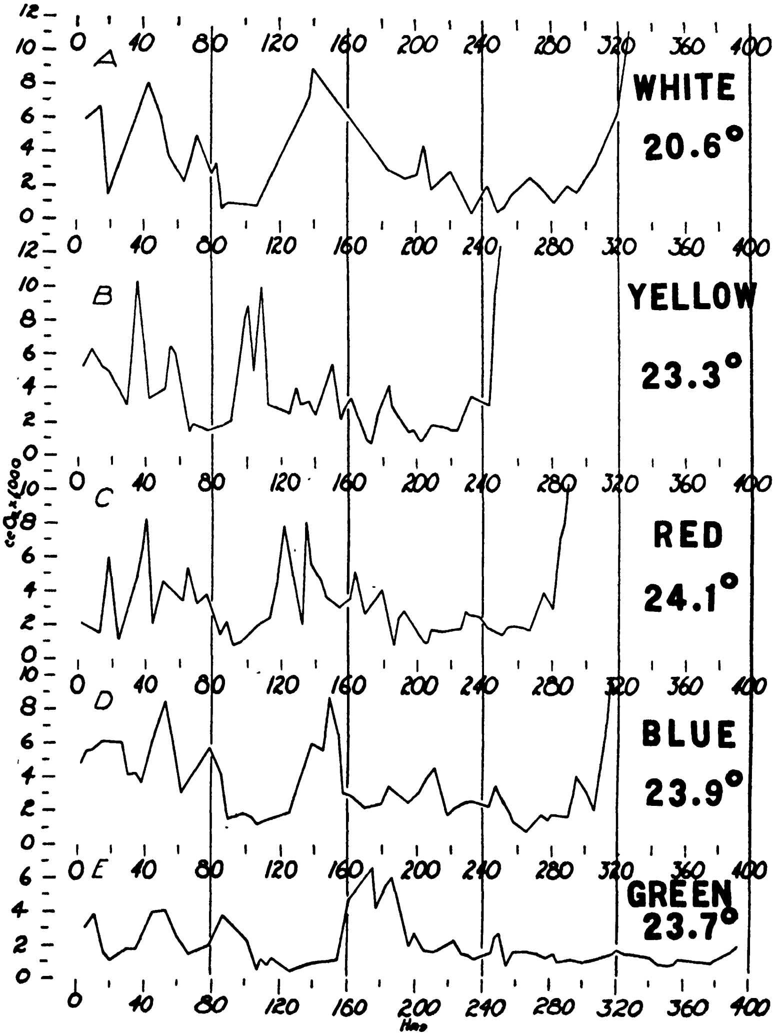

FIG. 8. Oxygen consumption under various light conditions.
A. White light, 20.6° C. B. Yellow light, 23.3° C. C. Red light, 24.1° C. D. Blue light, 23.9° C. E. Green light, 23.7° C.

region to define the developmental unit and to determine the total, measuring the remainder of the curve in these units. However, if this were done, no particular advantage would result, and the ease with which the entire curve could be compared with other data would be lost. Also, for purposes of definition the unit of development should be chosen from that portion of the curve nearer the middle of the range of viability.

As to the meaning of this shift in rate at about 14.5° C., it can only be said that evidence is accumulating that such a change represents a change in the nature of the chemical reaction limiting the rate of development (Needham, '31). As might be expected, such a change seems to be accompanied by an increased sensitivity of the embryo, evidenced by the sharp rise in the per cent mortality in this region of the temperature range (figure 6, B).

The upper portion of the curve shows the characteristic regression toward the temperature axis of all such curves beyond the optimum temperature range. The upper limit of viability probably is close to 36.5° C.

The medial range from 14.5° C. to 28° C. is longer and shifted higher on the temperature scale than is usual for aquatic organisms adjusted to a relatively low range of environmental temperatures. *Physa gyrina*, for instance, has a straight line portion of the developmental curve extending from 12° C. to 24° C.

The experiments dealing with radiation of different wave lengths show variations which have been demonstrated to be statistically significant in most cases, and which cannot be accounted for as a result of differential heating by absorption of radiant energy. If these differences in rate are considered only with respect to the number of hours to hatching at a given temperature, then the following relative effects are seen, taking for example the number of hours to hatching at 25° C.: Darkness, 201.5 hrs.; white light, 202.7 hrs.; red, 224.3 hrs.; yellow, 257.5 hrs.; blue, 296.3 hrs.; green, 356.1 hrs. The difference between the number of hours in darkness and in white light is not significant. All other light conditions, however, show a retardation, increasing in amount from 11 per cent in red to 27.5 per cent in yellow, 46.7 per cent in blue and 76.3 per cent in green.

When these data are analyzed on the basis of the temperature-velocity relationship for each light condition the differential effect is found to be the resultant of effects upon the *alpha* point as well as upon the rate of development. The alphas arranged in order of significance of difference from the darkness *alpha* (10.32° C.) are as follows: yellow (9.65° C.), green (9.57° C.), blue (9.47° C.), and white (11.80° C.). The *alpha* for red light is not significantly different from that for darkness.

The developmental totals, however, show another arrangement, as was discussed previously. The only two totals which do not differ significantly are those for darkness and for white light. The developmental total is a measure of the rate of development. As the total becomes numerically larger, the rate of development decreases, all other things being equal. It should be recognized that numerical variations in developmental totals do not mean that the total amount of metabolism necessary to complete the stage has changed. It means that the rate of development has changed, and as a result the size of the developmental unit measured in any absolute values, such as cubic centimeters of oxygen consumed, or carbon dioxide produced has changed. If the developmental total increases while the total amount of metabolism remains constant, then the amount of metabolism per unit decreases. In the case of green light the oxygen consumption total is noticeably lower than in the other experiments. This value comes closer to being significantly different than any of the others. It was observed, however, that in the late stages of development just before hatching a definite increase in activity, with a resulting increase in oxygen consumption, occurred. Under green light this prehatching increase in activity and oxygen consumption was definitely less than under other experimental conditions.

The situation, then, with regard to white light and darkness is that, although white light raises the *alpha* point significantly, the time of the developmental period is sufficiently long to prevent a significant retardation as long as the two rates are not different. The retardation in red light appears to be due entirely to the change in developmental rate, as the *alphas* do not differ significantly. In the case of yellow and blue light the *alphas* are lowered, but the lower rates of development more than compensate for this, and retardation results. The same is true for green light, but in this case a possible clue to the lowered rate of development is found in the oxygen consumption curves.

The outstanding feature of the oxygen consumption data is the sequence of modes, or peaks of consumption. These appear quite consistently in all kinds of light, except green, and at different temperatures. Table VII gives an analysis of the occurrence of these peaks, and also the elapsed fraction of total developmental time. It seems reasonable to presume that these peaks represent definite stages of metabolic increase during the course of development due to activity of the embryo or even periods of differentiation. The typical oxygen consumption curve, then, includes major peaks at .13, .22, .43, and .46, of the total development. Minor peaks occur at .04, .55, .62, .81, and .93 of the total. The curve also shows a sharp rise just preceding and during hatching, apparently due to increased activity at this time. The underlined values of table VII indicate corresponding peaks.

TABLE VII. *Modes of oxygen consumption in fractions of total development*

No.			Dark				White		Yellow		Red		Blue		Green	
	20.8°		20.8°		26.4°		20.57°		23.26°		24.09°		23.87°		23.73°	
	hr.	f.	hr.	f.	hr.	f.	hr.	f.	hr.	f.	hr.	f.	hr.	f.	hr.	f.
1	* 10	*.04*	* 11	*.04*	* 6	*.03*	* 14	*.04*	* 18	*.06*	* 8	*.03*	* 15	*.05*	* 10	*.03*
2	* 24	.08	* 19	.07	* 25	.14	* 42	.13	* 40	.14	* 36	.14	* 35	.11	* 52	.13
3	* 37	.13	* 32	.11	35	.19	* 71	.22	* 50	.17	* 55	.22	* 52	.17	* 86	.22
4	* 65	.23	* 62	.22	* 75	*.41*	* 83	.25	* 65	.22	68	.27	* 78	.25	109	.28
5	84	.29	* 71	.25	* 82	.44	90	.28	* 76	.26	101	.40	98	.31	115	.30
6	102	.35	83	.29	* 89	.48	*140	*.43*	88	.30	*109	*.44*	*138	*.44*	*174	*.45*
7	*121	*.42*	103	.36	*101	.55	*205	.63	*122	*.42*	*129	.52	*149	.47	*186	.48
8	*130	.45	*121	*.42*	*110	.59	*221	.68	*135	.47	137	.55	*184	.58	*199	.51
9	*138	.48	*130	.45	127	.69	243	.75	*164	.57	*151	.60	*211	.67	*223	.57
10	*156	.54	*138	.48	144	.78	*268	.82	*180	.62	162	.65	233	.74	*250	.64
11	*176	.61	*156	.55	157	.85	290	.89	193	.67	*184	.74	*248	.79	265	.68
12	194	.67	*176	.62	*172	*.93*	*299	*.92*	209	.72	199	.80	275	.87	283	.72
13	208	.72	197	.69	*185	1.00	*326	1.00	230	.79	209	.84	281	.89	294	.75
14	*225	.78	199	.70					258	.89	233	*.93*	*296	*.94*	321	.82
15	249	.86	206	.72					*276	*.95*	*250	1.00	*315	1.00	357	*.91*
16	269	*.93*	225	.79					*290	1.00					391	1.00
17	*288	1.00	250	.87												
18			*269	*.94*												
19			*286	1.00												

* = Mode above mean. hr. = hours after laying. f. = fraction of total time.

The oxygen consumption under the green filter is different from that under other light conditions (figure 8, E). The last third of the curve is flattened, the peaks are small and irregular and the characteristic sharp rise just preceding hatching is absent. This would indicate that an inhibiting effect of wave lengths in the green portion of the spectrum is present, decreasing activity or rate of metabolism during the latter part of development.

The failure of many eggs to hatch can be accounted for by the absence of the rise of metabolic rate and increase in activity usually preceding and probably essential to hatching. It has been stated, also, that the metabolic total in green light is low and the combination of a high developmental total, low rate, and low metabolic total, result in units of a smaller size (in cc. of oxygen) than under any other light condition. From the chemical point of view this would indicate an inhibiting effect of radiant energy transmitted by the green filter, directly or indirectly, on oxidation reactions in the embryo.

Unfortunately, the oxygen curves for other light conditions offer no definite evidence of the cause of the changes in metabolic rate which result in retardation, nor of the type of chemical reactions involved.

SUMMARY

An apparatus was constructed making it possible to raise eggs of *Helisoma trivolvis pseudotrivolvis* in running water under various light conditions at various temperatures. Colored glass filters were used to provide the light of different wave lengths; radiation intensity was measured by a thermopile and galvanometer, and regulated in such a fashion as to keep the radiation constant per unit of time, irrespective of the filter used. Thus, all eggs received about 1.31×10^{-3} gm. calories per cm.^{2} per hour.

Data were collected on rate of development at various temperatures under different light conditions. Darkness was considered the control. Temperature corrections were made for heat absorbed by the egg masses due to radiation. Oxygen tests were run, also, on samples of water collected from the apparatus so that rate of metabolism could be followed through the course of development. Retardation of hatching time occurred under all light conditions except white light. Darkness and white light produced no significant difference in hatching time or in developmental total, although the theoretical zeros of development were significantly different. The zeros for darkness and red were not significantly different; all others were. All developmental totals except white were significantly different from the total for darkness. The order of the lights with respect to amount of retardation in hatching time, from least to most, was red, yellow, blue and green. The order of the theoretical zeros, or *alpha* points from low to high was blue, green, yellow, dark, red and white. The order of the developmental totals from numerically low to high was dark, white, red, yellow, blue and green.

The highest rate of mortality was under green light. With respect to temperatures below the upper limit of the medial range, the highest mortality was between 10° C. and 15° C.

The oxygen consumption curves showed fairly consistent peaks of increased metabolic rate at intervals through the developmental period and a sharp rise just preceding and during hatching. Under green light these increases were smaller and more irregular during the last ⅓ of the developmental period, and the curve fails to show the characteristic rise at the end of development.

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BOTANICAL ANALYSES OF STOMACH CONTENTS AS A METHOD OF DETERMINING FORAGE CONSUMPTION OF RANGE SHEEP[1]

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Some areas of the western range are failing to maintain maximum production in the animals grazing on them. Because of this, numerous nutritional investigations are being conducted to determine causes of these abnormalities and to develop management methods to correct deficiencies.

Progress along these lines is hindered by lack of an adequate method for determining forage consumption by grazing animals. Attempts have been made to determine the diet by direct observation of grazing animals; however, this method is tedious and there is little correlation between the time an animal spends in grazing different species and the actual amount of forage consumed. Observation of grazed plants has also been used in estimating forage consumption, but this method is unreliable because it involves estimations of the species composition of the range and of the percentage of each species removed by grazing. These estimations are especially difficult on ranges composed of heterogenous vegetation and the results obtained are of limited application to studies in which the investigator requires accurate information on the species composition of the animal diet.

Analyses of the stomach contents have been used widely in wildlife research as an indication of the diet of animals. However, no studies involving feeding known rations with subsequent botanical analysis of the stomach contents have been conducted to determine the accuracy of stomach analyses data.

REVIEW OF THE LITERATURE

Various methods for determining approximately the forage consumption of grazing animals have been suggested. Schuster ('29) listed thirteen different methods for estimating forage eaten. Garrigus and Rusk ('39) developed a consumption-defecation ratio method for measuring the forage consumption of grazing steers. Cory ('27) observed every action of grazing animals throughout a 24-hour day to obtain information concerning the behavior and feeding habits of range livestock. Dixon ('34) followed deer and noted the time spent grazing upon each plant species. Snow trailing and stomach analyses have been used by the Colorado Game and Fish Commission ('41) to estimate forage consumption of deer. Little investigation on stomach analyses of sheep as a measure of forage consumption has been attempted.

Passage of food through the digestive tract has been studied primarily in cattle, although Forbes *et al.* ('37) have found sheep to be similar, except that they digest somewhat more efficiently and rapidly. The food soaks and ferments for 12 to 24 hours in the rumen, then rumination occurs and the food is regurgitated and remasticated. After this, the finely ground food material passes directly from the rumen to the omasum (Amadon, '26; and Ritzman, '38). In steers, food requires 61 hours in passing through the rumen, 7.9 hours in passing through the omasum, and 2.8 hours in the abomasum (Ewing and Wright, '18). Corn and alfalfa hay, whether ground or whole, fed

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[1] The author wishes to express his sincere appreciation to Dr. L. A. Stoddart for his encouragement and assistance during development of the problem and preparation of the manuscript.

Authorized for publication by the Director, Utah Agricultural Experiment Station, July 15, 1942.

to cattle shortly before slaughter, is all found in the rumen (Dukes, '35). In sheep, 32.1 per cent of the rumen dry matter is digested within 3 hours, 48.5 per cent within 6 hours, and 58.8 per cent within 9 hours (Rathnow, '38), and food begins to pass from the rumen to the omasum within 2 to 5 hours after ingestion. Emptying of the rumen is complete in 8 to 12 days (Columbus, '34). The state of the ruminal contents differentiates sheep starved for 24 hours from those starved 40 to 48 hours. After a 24-hour starvation period the contents are semi-solid in the majority of cases, after 40 to 48 hours starvation the contents are fluid or watery, and in unstarved animals they are solid or semisolid (Ross, '34).

Brünnich and Winks ('31), in Queensland, attempted to utilize chemical analyses of the paunch contents as a measure of the diet of animals. Their results showed wide differences between the composition of the paunch contents and of the ration fed. Parrish ('41), at the Utah Agricultural Experiment Station, conducted chemical studies on the paunch contents of the sheep used in the present investigation and his findings generally concur with those of Brünnich and Winks. A brief summary of Parrish's results are included later in this report.

DeNio ('38) stated that a detailed botanical analysis of the stomach contents of deer and elk is a methodical and mathematical system by which identification of forage utilized is possible. It was also possible to ascertain the relative proportions of each forage species utilized through determination of percentages by weight or volume of forage species represented. He recommended standardization of size of sample analyzed at two per cent of the air-dry weight of the total rumen contents. Rush ('32) stated that examination of the stomach contents of elk to determine the plants consumed is useful but, because of the fragmentary condition of all the plants in the stomach, it is difficult to identify species.

Methods used in stomach analyses are generally similar and consist of washing the material and separating the particles of each constituent by washing, decantation, screening, or picking out with forceps. A microscope is used to aid in the identification of small fragments, and the percentage of each constituent is determined. Percentage by volume is more commonly used than percentage by weight (Cottam, '36; Hosley and Ziebarth, '35; and McAtee, '21).

DEVELOPMENT OF THE METHOD

Since no previous work of a similar nature had been conducted it was necessary to develop a procedure for feeding animals and handling the stomach contents. In preliminary trials, animals were placed in small pens and fed a known ration for a period of three days in an attempt to clear the paunch of residue from previous feedings. Following this, no feed was given for 24 hours. Then the animals were fed a weighed amount of the same forage, slaughtered, and the contents of the rumen and reticulum removed. It was recognized that a 24-hour starvation would not empty the paunch. However, it was desired to keep the animals as near normal in food consumption and digestion as possible. A longer starvation period would have caused abnormal consumption and interfered with digestion. That portion of the ration not consumed was recovered, separated, weighed, and consumption of each constituent calculated. Feeding in open pens allowed the sheep to scatter food underfoot so that it was difficult to recover. Therefore, subsequent animals were placed in crates large enough to permit an animal to lie down but not to turn around. The animals could feed by extending the head into a removable box outside the crate. This method facilitated collection of feed not eaten and was used for all subsequent sheep.

The contents of the paunch were weighed, thoroughly mixed, and a sample for moisture determination was taken. The remaining material was washed on a window screen and all the finely comminuted particles which passed through were collected on a bolting cloth. It was found that this material was too small to warrant separation so it was weighed but not subsequently analyzed. The remainder on the screen was dried, a representative sample of two per cent of the total was taken, and all the readily identifiable particles were picked out with forceps. The remaining fragmentary material, which could be separated only by tedious work too time-consuming to be practical, was grouped as unseparated. The percentage of each forage found in the stomach was compared with the percentage in the ration as a measure of the efficiency of stomach analyses in measuring forage consumption. The dry weight of each plant fed also was compared with the amount recovered in the stomach, calculated from the percentage in the sample and the total stomach contents. Although some investigators on stomach analyses consider estimated percentage by volume to be more satisfactory, percentage by weight was used in these experiments because the ration fed was calculated on a weight basis. Further, weight seems a more logical measure than volume in addition to eliminating error in estimating volume percentage.

To test the accuracy of this method of identifying stomach contents, the contents of seven bison stomachs were analyzed and were later sent to the U. S. Fish and Wildlife Service laboratory in Denver, Colorado for analysis by an experienced analyst. Close agreement was obtained in the two analyses, indicating that the present method has an accuracy comparable to that of usual experimental procedure.

EXPERIMENTAL PROCEDURE

The sheep used in this investigation were a varied group of 19 animals, chiefly Rambouillet, to which three different types of forage were fed. Two sheep received fresh, green plants collected in the fall while two others were fed highly succulent plants collected in early spring from foothill ranges near Logan, Utah. Nine sheep were fed rations of cured hays and six received dry desert plants collected from winter ranges near Milford, Utah. The latter were range animals familiar with desert vegetation. They had been receiving a ration of good pasture hay for a short time and the 3-day preliminary feeding period was not used.

RESULTS AND DISCUSSION

There appear to be two logical methods of approach to analyzing the data obtained from stomach analyses. One system is to compare the amount of each forage consumed with the actual amount separated from the stomach contents. Another method is to assume that the unseparated material is of the same percentage composition as the separated portion, which gives a theoretical figure of the percentage composition of the entire stomach contents. The percentage of each forage in the ration may then be compared with the theoretical percentage in the stomach, or the weight consumed by the animal may be compared with the theoretical weight in the stomach. These methods of study have been used for all the data obtained from the nineteen experimental animals and the average results are presented in table I.

It is apparent that varying amounts of coarse forages will remain in the stomach for at least four days as evidenced by the presence of straw in the stomachs of the sheep fed green fall forages. These animals had been kept in pens bedded with straw prior to the experimental period, but they were removed four days previous to slaughter. The same is true with the sheep fed green spring forages which had been receiving barley prior to the experiment; straw and barley grain

TABLE I. *Average consumption of forage and composition of stomach contents of experimental sheep fed six different experimental rations*

	Amount consumed	Composition of ration	Actual stomach contents	Theoretical stomach contents *		
	grams	*per cent*	*grams*	*grams*	*per cent*	*per cent of fed ration* †
Green Fall Forages						
Lactuca scariola	51.15	13.99	40.25	115.11	15.14	19.55
Malva rotundifolia	83.65	22.87	50.89	145.32	19.14	24.71
Melilotus alba (clover)	74.80	20.45	37.09	106.49	13.98	18.01
Mixed grass	156.15	42.69	77.68	220.75	29.12	37.73
Straw			60.15	146.85	22.62	—
Unseparated			493.45			
Green Spring Forages						
Alfalfa	71.95	28.60	36.17	90.17	29.67	39.33
Poa pratensis	100.55	39.96	34.29	84.93	27.93	37.28
Lactuca scariola	47.20	18.76	10.92	26.69	8.79	11.87
Malva rotundifolia	23.65	9.40	6.73	16.70	5.50	7.32
Eurotia lanata	8.25	3.28	3.86	9.73	3.21	4.20
Barley and straw			31.30	75.30	24.90	—
Unseparated			180.25			
Mixed Ration No. 1						
Alfalfa hay	200.4	62.31	94.91	184.13	51.86	—
Grass hay	121.2	37.69	91.88	170.95	48.14	—
Unseparated						
Mixed Ration No. 2						
Alfalfa hay	68.0	27.59	80.27	171.91	52.13	—
Grass hay	161.0	65.31	69.97	149.95	45.47	—
Corn silage	17.5	7.10	3.64	7.94	2.40	—
Unseparated			175.92			
Mixed Ration No. 3						
Alfalfa hay	118.5	47.78	115.05	216.29	52.50	—
Grass hay	89.0	35.89	94.76	178.64	43.36	—
Eurotia lanata	40.5	16.33	8.99	17.03	4.14	—
Unseparated			193.66			
Desert Forages						
Oryzopsis hymenoides	119.5	49.71	134.81	348.55	57.75	70.39
Eurotia lanata	70.7	29.41	31.24	80.97	13.41	16.31
Atriplex canescens	50.2	20.88	25.48	66.89	11.08	13.30
Grass hay			40.52	107.18	17.76	—
Unseparated			371.79			

* Theoretical in that unseparated material was considered to have the same composition as separated material.

† Percentage composition based upon separated material of plant species actually fed.

were found in all stomachs although none had been fed for four days. The sheep fed desert forage plants received grass hay prior to a 24-hour starvation preceeding experimental feeding, and varying amounts of this material were found in all stomachs. Results of this nature indicate that stomach contents are an inaccurate measure of the forage consumed by animals immediately before slaughter.

In some cases, a greater amount of certain forages was recovered in the stomach than was fed at the final feeding. This was true with alfalfa hay in the sheep fed mixed ration no. 2, and grass hay in the sheep fed mixed ration no. 3. The sheep fed desert forages showed a larger amount of *Oryzopsis hymenoides* than was fed. These excesses in the stomach over the amount fed may indicate inaccurate sampling of the stomach contents, but more likely they signify that various amounts of the residues from previous feedings remain in the stomach and confuse the analysis.

Most of the results reveal that more material was fed than was separable from the stomach contents. This was expected since over half of the stomach contents consisted of material too fragmentary for separation. It also may indicate that digestion in the stomach continuously removed material, causing the quantitative analysis to be in error. The four sheep fed green forages showed rather consistently a lesser amount of each plant separated from the stomach than was fed. Since these animals received succulent plants, it appears that there is a rapid passage of fresh, green material through the stomach. Results of this nature, showing that in some cases more of certain forages was found in the stomach than was fed, while in others, less was found than fed, indicate differences in the rate of digestion of various forages. Several instances showed that a differential in the digestibility of forages may cause disproportionate amounts to appear in the stomach. This is particularly apparent in the sheep fed green spring forage plants where a decidedly lesser percentage of the *Poa pratensis* which was consumed was found in the stomach than was true of alfalfa. Similarly, in sheep fed desert forages a lesser percentage of the *Atriplex canescens* which was consumed was found in the stomach than was true in the case of *Oryzopsis hymenoides*. Similar variabilities were apparent between different sheep fed like diets, suggesting a differential in their digestive capacities.

Comparison of the percentage of each forage in the ration with the theoretical percentages of each found in the stomach shows considerable disagreement, indicating that the unseparated material cannot be assumed to be of the same percentage composition as the separated material and that the percentage of a forage found in the stomach is a poor measure of the percentage in the diet. Generally, the theoretical amounts of all constituents in the stomach were greater than fed, again showing the presence of residue from previous feedings.

The results showed extreme variability between sheep and between forages so that it was not possible to calculate a correction factor to eliminate the effects of digestion and previous feedings.

Some interesting data were obtained by Parrish ('41) in connection with the present study. He made chemical analysis of the rations placed before the animals and the feed rejected by the animals, and thus was able to calculate the exact composition of the feed consumed. This was compared to the composition of the stomach contents to determine whether such analysis could be used as an index to the diet composition (table II).

It is apparent that a smaller percentage of crude protein was found in the stomach than in the ration fed where the experimental animals received diets of green forages. The reverse was true when mixed rations of dry forages were fed. This may indicate that the protein in green forages passes from the stomach at a relatively rapid rate, whereas, the protein in dry forages passes more slowly. In general, a higher percentage of crude fat was found in the stomach contents then in the ration. The results with crude fiber were variable, perhaps because of differences in the digestibility of different rations and the digestive abilities of different animals. Nitrogen-free extract was lower in the stomach contents than in the ration fed while ash was higher in the stomach in all cases. Apparently the nitrogen-free extract passes

TABLE II. *Average chemical composition of the ration and of the contents of first two stomachs of sheep fed five different experimental forages expressed in per cent.* Data from Parrish ('41)

Forage	Crude protein		Crude fat		Crude fiber		Nitrogen-free extract		Ash	
	In ration consumed	In stomach contents	In ration consumed	In stomach contents	In ration consumed	In stomach contents	In ration consumed	In stomach contents	In ration consumed	In stomach contents
					per cent					
Green fall forages......	19.53	13.41	3.74	3.16	23.18	30.04	41.01	32.43	12.54	20.98
Green spring forages....	23.60	18.70	3.33	30.24	21.92	11.11	35.71	22.81	15.42	17.15
Mixed ration no. 1.....	12.29	17.25	2.09	4.18	30.55	31.03	47.43	30.76	8.02	16.78
Mixed ration no. 2.....	10.03	14.95	1.38	2.82	33.36	36.63	47.30	29.97	7.70	15.64
Mixed ration no. 3.....	12.46	13.50	1.87	4.14	31.29	28.75	46.29	39.30	8.05	14.32

through the stomach rapidly, whereas ash tends to accumulate.

Comparisons of the weight of each constituent consumed with the weight of each recovered in the stomach always showed much more present in the rumen and reticulum than was consumed in the final ration in the case of each constituent, excepting nitrogen-free extract. Even in this case, many stomachs showed larger amounts than were present in the ration.

CONCLUSIONS

The wide variability of the results throws considerable doubt upon the value of stomach analyses as a measure of the diet of grazing animals. It is evident that residues from previous feedings remain in the stomach and confuse the analyses and that certain types of forage pass through the stomach at a more rapid rate than do others. This lack of consistency in the comparisons between the forage fed and that found in the stomach indicated differences in the rate of digestion of various forages. A similar lack of consistency between different sheep fed comparable rations points toward differences in the digestive capacities of sheep.

The fact that no consistent relationship existed between the amount of forage fed and that found in the stomach indicated that stomach analyses are of limited value in measuring the amounts of different forages eaten by sheep. However, since it was possible to identify portions of all the forages fed, there is some promise of stomach analyses as a qualitative indication of the diet. Analyses of stomach contents will be useful in compiling a list of plant species consumed by grazing animals. It has been pointed out that succulent forages pass through the stomach rapidly, whereas, dry, woody materials digest slowly and, because of this, caution must be used in interpreting results of qualitative stomach content analyses. It is apparent that certain forages eaten several days previously may appear in the stomach while highly succulent material consumed shortly before slaughter may not be identifiable. Hence, stomachs may show large percentages of coarse browse which has been eaten over a period of days leading the analyst to conclude that browse is the chief article of the diet, while, in reality, rapidly digested, succulent forage may have been consumed in much larger amounts.

These results show that stomach analyses of sheep are of limited value in measuring forage consumption. Similar results may be expected in other ruminating animals; hence, stomach analyses must be used with care and only in connection with other methods of diet determination. With birds and rodents or animals having digestive systems differing from the type in ruminants, stomach analyses may prove more precise.

The results of chemical analyses of stomach contents reported by Parrish ('41) appear to show that such analyses are of limited value as an index to the diet of sheep. This substantiates findings of botanical analyses in that differences in digestibility of forages and the digestive abilities of sheep tend to make the stomach contents unrepresentative of the forage consumed and, in addition, the chemical analysis is confused by the presence of digestive juices.

SUMMARY

Botanical analyses of the stomach contents of nineteen sheep have been made to determine the accuracy of the method as a measure of the diet of grazing animals.

The sheep were starved 24 hours, fed weighed amounts of various forages, slaughtered, and the stomach contents removed. The contents were washed, screened, dried, and a sample of two per cent of the total was analyzed. Recognizable particles of each forage were picked out and weighed to determine the percentage by weight of each species. Fragmentary material, too small to warrant separation, was grouped as unseparated material. The amount of each forage found in the stomach was then compared with the amount in the ration as a test of accuracy.

Wide variability between the amount of each forage fed to the animals and the amount found in the stomach throws considerable doubt upon the value of stomach analyses as a quantitative measure of the diet of grazing animals. Varied amounts of material from previous feedings remain in the stomach and confuse the analyses. Differentials in the digestibility of different forages and variations in the digestive abilities of sheep were found.

From a qualitative standpoint, stomach analyses show some promise and may be used, in connection with other methods of food habit studies, to compile lists of plant species eaten by grazing animals. However, the results throw great doubt upon the accuracy of the method as a means of determining the actual amount of each forage making up the diet of ruminants.

Chemical analysis of stomach contents compared to that of forage consumed showed results even more variable than those from botanical analysis and it is doubtful if this method is of any value as an index to the composition of the diet of grazing animals.

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THE PALATABILITY OF FRESHLY FALLEN FOREST TREE LEAVES TO MILLIPEDS

WALTER H. LYFORD, JR.[1]

Millipeds are quite widely distributed throughout the forests and cultivated lands of the Northeast, and they are of some importance in the decomposition of the forest floor and in the incorporation of organic matter into the upper soil layers. Romell ('35) has noted the importance of a large species, *Fontaria trimaculata* (Wood), in the formation of one type of mull and Heiberg and Chandler ('41) have indicated that millipeds are rather common in fine mull. The fact that mulls permit rapid infiltration of water thereby minimizing soil erosion is well known and the action of millipeds is, therefore, of importance not only from the standpoint of favorable forest growth but also from the standpoint of the conservation of the soil.

This present study was conducted by the use of the common brown milliped, *Diploiulus londonensis caeruleocinctus* (Wood),[2] an European form, long established in the Eastern United States and Canada, and the aim of the study was to discover:

(a) The time of year when millipeds are most active.

(b) Which tree leaves are most desirable as food to millipeds.

(c) How palatability of the leaves varies with soil type.

(d) How palatability of the leaves varies with the amount of ash and calcium present.

The importance of millipeds in the decomposition of the forest floor should not be over estimated. Millipeds, in general, probably do not devour more than one to five per cent of the forest floor except in isolated areas, and, no doubt, they are of less importance in this respect than are earthworms and minute insects. Nevertheless, the results of this study may be of value because it suggests a rather rapid laboratory method for studying the relative palatabilities of tree leaves to one species of forest floor inhabitant and shows how the palatability of several tree species of economic importance varies with the soil type.

These data have practical application providing the hypothesis is made that the leaves which are most palatable to millipeds are also most palatable to the more numerous forest floor invertebrates. The close connection between the presence of mulls and certain forest trees, (Chandler, '39, '41), the prevalence of fauna in certain types of forest floor, and the likes and dislikes of earthworms, (Gast, '37), (Johnston, '36), would seem to furnish grounds for believing that this hypothesis is tenable.

EXPERIMENTAL PROCEDURE

Collection of millipeds.—The millipeds used, *Diploiulus londonensis caeruleocinctus* (Wood), were almost perfectly cylindrical, about three millimeters in diameter and chocolate brown in color. They were active only in the dark and coiled up characteristically when touched, the head remaining on the inside of the coil.

Collection of millipeds in fairly large numbers was possible because of their prevalence in an area of Paxton fine sandy loam on which runoff plots were installed. Galvanized tanks and concentrating devices were set up at the lower end of each of seven runoff plots in order to catch the soil and water which ran off following rains. A number of the millipeds crawled into the tanks during the nights and were unable to crawl out because of the smoothness of the galvanized metal. They were collected and counted at frequent intervals and were stored in a smooth-sided container.

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[2] Identification of the milliped and the information about its range were kindly made by R. V. Chamberlin, University of Utah.

Leaf collections.—A laboratory method was used to determine the palatability of the freshly fallen forest tree leaves to millipeds.

Leaf collections were made just after the leaves had fallen and before the weather had a chance to influence their composition. Approximately 50 leaves were collected from under each tree.

Four sites, one on each of four soil types, were chosen for sampling in 1940. The leaves of one tree of each species of the deciduous forest trees growing on each site were collected.

The four soil types used in 1940 were Colrain fine sandy loam, Gloucester fine sandy loam, Paxton fine sandy loam, and Hermon sandy loam. The first three are members of the Brown-Podzolic great soil group, while the Hermon sandy loam is a member of the Podzol great soil group. All are developed from glacial till and are well drained.

Colrain fine sandy loam developed from till derived from a weakly calcareous mica schist. The profile of the soil is acid throughout but occasional bands of limestone may be found in the bedrock which lies in most places within four or five feet of the surface.

Paxton fine sandy loam developed from till derived from a non-calcareous mica schist and is characterized particularly by a compact substratum which occurs at a depth of about 20 inches.

Gloucester fine sandy loam developed from till derived from granite and gneiss and the soil profile is loose and porous throughout.

Hermon sandy loam was developed also from granitic and gneissic till but is found in a cooler climate and at a higher altitude than Gloucester.

The results obtained from the 1940 leaves indicated that the number of samples should be greater in order to obtain a true picture of the actual palatabilities. Consequently, two sites on each soil type were chosen for sampling in 1941. Collection of leaves was not limited to one tree of each species, as it was in 1940, and as many as four trees of each species were sampled on some sites in 1941. Therefore, duplicates were available for each soil type as well as for the species on each site.

The four soil types sampled in 1940 were used in 1941, but, in addition, leaf collections were made from species growing on Marlow fine sandy loam which is the Podzol relative of the Paxton fine sandy loam.

Method for testing palatability.—Ordinary glass laboratory moisture chambers served the dual purpose of caging the millipeds and providing sufficient moisture for keeping the leaves damp.

About one-half to three-quarters of an inch of moist topsoil was placed in the bottom of the moisture chamber. The soil was covered by a 4-mesh galvanized screen cloth bent at the edge so as to keep the cloth suspended about one-quarter inch above the surface of the soil and the leaves were placed on top of the screen. The space between the screen cloth and the soil allowed plenty of room for free movement of the millipeds and prevented direct contact of the leaves with the soil. In preliminary trials it was found that leaves which were placed on the soil surface itself sometimes were eaten in preference to those which were not in contact with the soil regardless of their relative palatability.

Two hundred millipeds were counted out and put in duplicate moisture chambers and the leaves added. Several trials made with varying numbers of leaves showed that two leaves from each tree provided fairly comparable results. Fifty leaves could be placed in each moisture chamber without being crowded and when only two leaves from each tree were used, it was possible to compare the palatabilities of leaves from several species of trees at the same time.

Two entire leaves from each tree on the site were selected and dipped for about ten seconds in water. The excess water was then shaken off and the leaves were well mixed and placed in the moisture chamber on top of the screen cloth. Leaves from different trees of the same species were identified conveniently by attaching colored string to the petioles.

The moisture chambers were left on a shelf in the laboratory and the first observations were made in from two to four days, with subsequent observations at four-day intervals. The amount of leaf material eaten by the millipeds was determined by removing the leaves from the moisture chamber and recording the percentage of leaf area of each species consumed. Those leaves which had been largely consumed or whose relative palatability could be judged without question were removed and the remaining leaves were put back in the moisture chamber. If the most palatable leaves were left in the moisture chamber the millipeds fed on them to the exclusion of the others and the trial had to be carried on over a much longer period of time.

The relative palatability of the leaves was determined by the amount which had been eaten in a certain time interval. The actual amount of area consumed was calculated from the percentage of leaf area eaten and the total area of the leaves. Duplicate moisture chambers were used for the leaves from each site. The results obtained from the duplicates agreed fairly well, as is shown in table 2.

Determination of per cent ash and per cent calcium.—The determination of the average per cent ash and the average per cent calcium in the leaves of each species of tree was made on a composite sample. This composite sample was made by combining the samples used for the determination of palatability. Equal weights of leaves from each sample of the same tree species were taken, regardless of soil type, and these leaves were combined into one large sample.

The leaves were ground in a Wiley knife mill and were dried out at 80° C. for twenty-four hours. Per cent ash was determined by ignition at cherry-red heat. The ash was treated with 2N HCl and the calcium content was determined by the method of Frear and Kahlenburg ('33).

Experimental Results

Migration and activity of millipeds.—The millipeds were collected from runoff plots which had been established for the purpose of making a study of erosion resulting from various methods of growing potatoes. The area had been in sod for a number of years at the beginning of the experiment and potatoes were grown on six of the plots in order that the common practice of growing potatoes for several years on the same area would be followed. Inasmuch as this species of milliped sometimes causes injury to potatoes (MacLeod and Butcher, '34), counts were made over a two-year period in order to get an idea as to their harmfulness in the present instance. They have not yet been found harmful to the potatoes but the counts have provided information of the time of year when the millipeds are active. Seasonal activity is important from the standpoint of the forest floor because this species of milliped seems to be more numerous in forest soils than in agricultural soils.

The number of millipeds collected on each of the seven runoff plots at typical seasons of the year is presented in table I. These data indicate the variation between plots. One must bear in mind that the number of millipeds collected may be only slightly correlated with the actual number of active millipeds because varying numbers of the millipeds may have turned back when they reached the edge of the tanks.

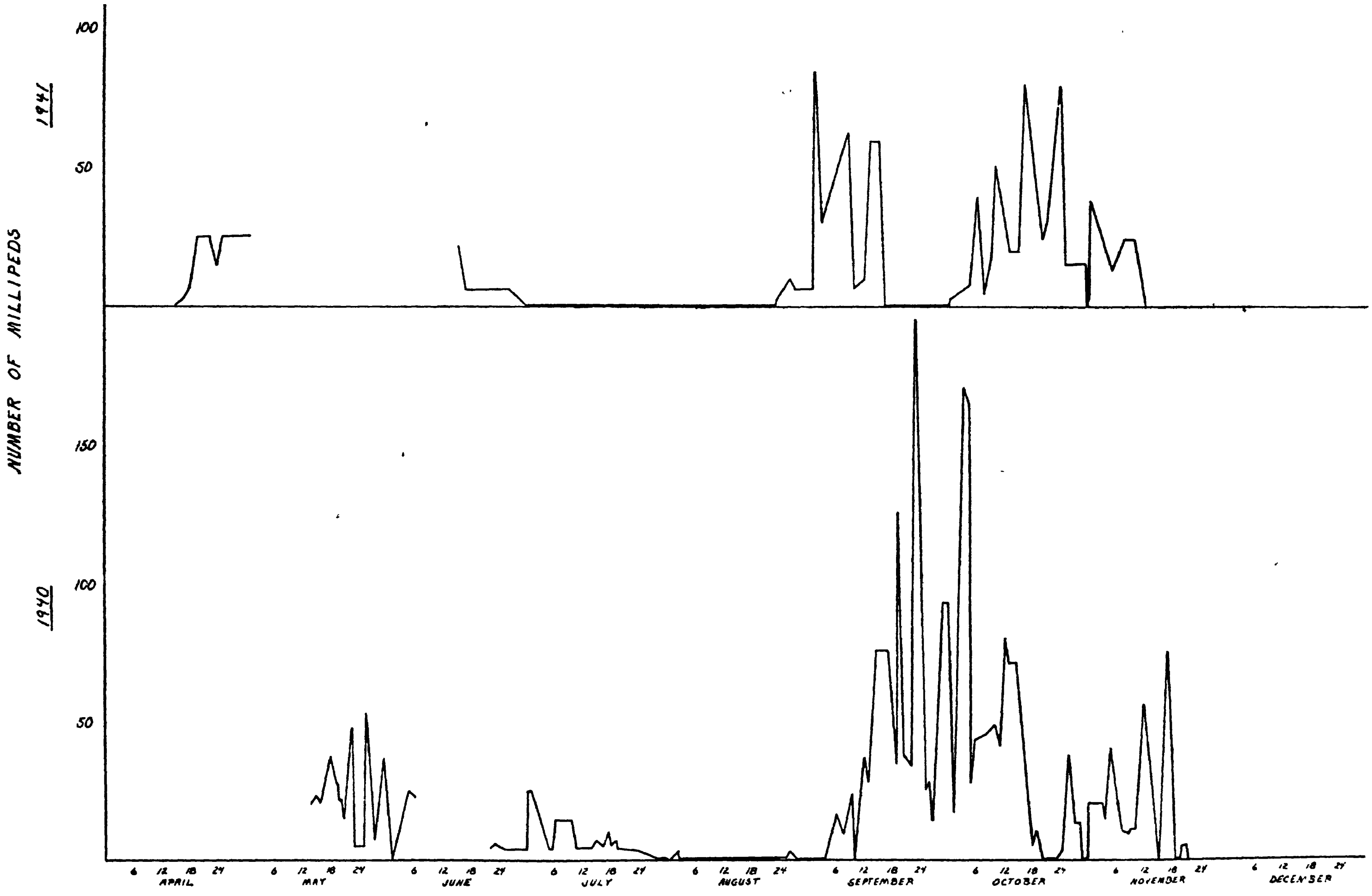

FIG. 1. The relationship between the time of year and the activity of millipeds for the years 1940 and 1941 as judged by collections from the runoff plots.

TABLE I. *Numbers of millipeds collected from the run-off plots at typical seasons of the year*

Date	Grass Plot	Cultivated Plots					
		1	2	3	4	5	6
May 29, 1940	11	4	4	1	1	3	8
May 30	47	18	22	34	18	46	63
May 31	28	17	31	24	12	42	33
July 14	8	12	8	1	1	2	5
July 15	4	0	11	1	0	5	12
Sept. 17	164	4	70	0	29	20	75
Sept. 18	335	9	180	19	124	40	390
Sept. 19	375	8	165	33	100	25	235
Nov. 15	2		3	2	1	0	2
Nov. 16	37		63	43	46	101	138

The activity of the millipeds throughout the years 1940–41, as judged by the average number collected from the six cultivated plots, is shown in figure 1. The breaks in the curve show the periods when counts were not made.

This graph shows that milliped activity starts as soon as the frost is out of the ground and continues moderately until about the middle of July. Activity then ceases until about August 25. Activity from August 25 increases immediately and reaches a maximum during September and October. The activity during this period is definitely limited by the dry condition of the soil. This is indicated to some extent by the fewer number collected during a dry period in the latter part of October, 1940, and is more definitely indicated by the actual cessation of activity during the unusually dry period of the latter part of September, 1941. The cessation of activity in 1940 during July and August is not caused by dry conditions because soil moisture was not limited during this period. However, soil moisture was limited during the summer of 1941 and the longer period of inactivity in this year may have been occasioned, in part, by the lack of rain.

Activity ceases in the fall when the soil freezes.

In general the number of millipeds collected was greatest from the grass plot. The abundance was roughly parallel to the average numbers collected from the six cultivated plots except for the period immediately following the beginning of activity in April, 1941, when for several nights 150–200 millipeds per night were collected from the grass plot.

Millipeds migrate at times in such large numbers that some mention of local migrations is found in the literature (Back, '39), (Brooks, '19). The cause of the migration is not known but it may be related in some manner to the hatching of the young. Observation of the millipeds collected following the quiescent period during August, 1941, showed that a considerable proportion of those from one or two of the plots were definitely immature.

The cause of the variation in number of millipeds collected from night to night is not known. Millipeds were not active during rains but this accounts for only a small part of the variation shown on the graph. Neither temperature nor humidity differences seem consistently

TABLE II. *Variation in palatability of elm and ash leaves collected from several trees on Gloucester fine sandy loam* *

Percentage of Leaves Eaten

Species	Tree	October 24		October 27		October 31	
		Chamber No. 1	Chamber No. 2	Chamber No. 1	Chamber No. 2	Chamber No. 1	Chamber No. 2
Elm	1	7.0	15.0	40.0	70.0[1]	50.0	70.0
	2	5.0	15.0	70.0[1]	40.0	85.0	60.0
	3	1.0	1.0	5.0	5.0	15.0	10.0
	4	1.0	2.0	20.0	20.0	40.0	70.0
Ash	1	5.0[3]	20.0[2]	30.0	40.0	30.0	50.0
	2	5.0[3]	0.0	20.0[3]	10.0	40.0	30.0
	3	0.0	0.0	5.0[3]	0.0	10.0[3]	10.0[3]
	4	0.0	0.0	5.0	2.0	30.0	20.0

[1] Two leaves 100 per cent eaten.

[2] Two leaves eaten.

[3] One leaf eaten.

* Three leaves from each tree used in the moisture chamber. Two hundred millipeds used in experimental setup, October 21, 1941. Unless otherwise noted, all three leaves were eaten in about the same proportion.

related to the numbers of millipeds collected.

Variation in palatability of leaves from the same tree.—From the data it appears that there was some variation in the avidity with which leaves from the same tree were eaten by millipeds. Occasionally a leaf was absolutely refused as food whereas the companion leaf was readily accepted. Some idea of this variation may be obtained from a study of table II. In general, however, the variation in palatability between individual leaves from the same tree was not as great as the variation between leaves from different trees of the same species.

Each leaf seemed to have some parts which were more desirable as food, because the entire parenchyma was eaten only on the most palatable leaves. No particular part, however, was consistently favored and, in most instances, at least 90 per cent of the area would be eaten in time. From figure 2 some idea may be obtained about the condition of the leaves after being eaten by the millipeds.

TABLE III. *Palatability of leaves collected on Hermon sandy loam 1941-A*

Tree Species	Sq. Mm. of Leaf Area Eaten per Milliped per Night
Yellow Birch No. 1	4.7
Yellow Birch No. 2	4.4
Ash No. 2	4.3
Ash No. 1	3.6
Large-toothed Aspen	3.1
Red Maple No. 2	2.5
Red Maple No. 1	2.0
Sugar Maple No. 2	1.5
Paper Birch	1.2
Sugar Maple No. 1	0.7
Gray Birch	0.6
Red Oak No. 1	0.3
Red Oak No. 2	0.0
Beech No. 1	0.0
Beech No. 2	0.0

Variation in palatability of leaves from adjacent trees of the same species.—Leaves of the same species from adjacent trees show some variation in palatability

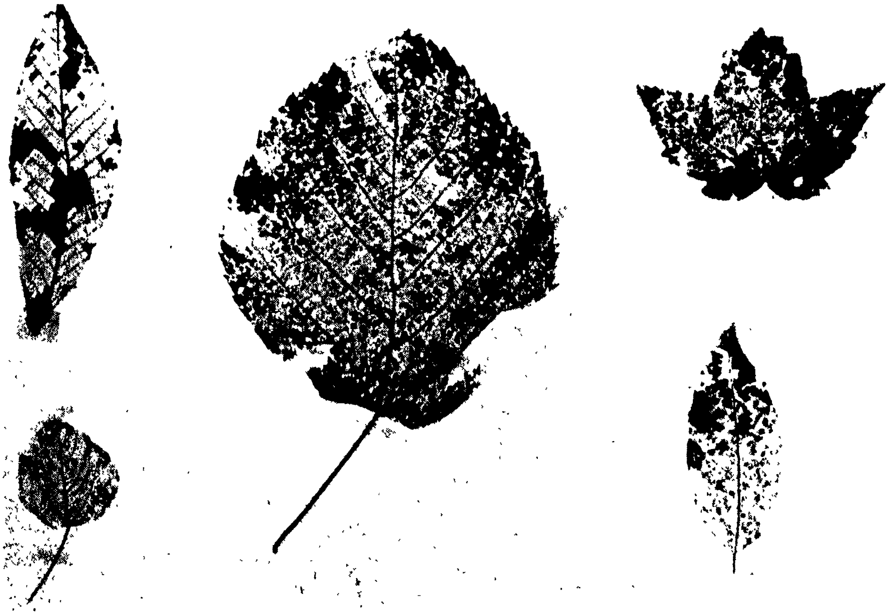

FIG. 2. Tree leaves showing the results of feeding by millipeds.

Shag-bark Hickory

Trembling Aspen

Basswood

Red Maple

White Ash

to millipeds. Occasionally the leaves of one tree may be quite different from that of the average. The variation for one such tree (Elm No. 3) is shown in table II.

Variation in palatability of leaves from different species of trees growing on the same site.—Table III presents the results obtained from a run on the leaves collected from all the species of forest trees on one of the Hermon sandy loam 1941 sites. The trees are listed from top to bottom in the order of leaf preference.

Table III shows that leaves from the same species of tree are of about the same palatability and also that the leaves of some tree species are considerably more palatable than others.

Variation in palatability of leaves growing on different soil types.—Leaves from different sites on the same soil type varied quite widely in their palatability even though leaves from two or more trees of each species on each site were used. In fact the range of values was so large that any differences in the palatability of leaves of the same tree species from the five different soil types were not statistically significant and so the results are not tabulated here. Whether differences due to soil type would show up if more trees and sites had been used is questionable. The leaves from Colrain fine sandy loam seemed to be somewhat more palatable than the leaves from the other four soil

TABLE IV. *Average palatability, per cent ash, and per cent calcium, of the leaves of several species of forest trees*

Tree Species	Number of Trees	Sq. Mm. Eaten per Milliped per Night	Range of Values	Average Per Cent Ash, Oven-Dry Basis	Average Per Cent Calcium, Oven-Dry Basis	Group
Basswood (*Tilia americana* L.)	5	13.85	5.65–24.20	7.69	2.78	1
Striped maple (*Acer pennsylvanicum* L.)	4	8.99	1.19–17.70	7.50	1.58	1
Elm (*Ulmus americana* L.)	12	7.37	1.68–15.3	11.20	1.76	1
Shag-bark Hickory (*Carya ovata* (Mill.) Koch.)	6	5.68	3.20–13.20	7.09	1.88	1
Chestnut (*Castanea dentata* Borkh.)[1]	3	4.47	1.85–7.95	5.64	1.21	2
Speckled Alder (*Alnus incana* [L.] Moench.)	3	3.84	2.18–4.89	2.74	0.71	2
Yellow Birch (*Betula lutea* Michx. f.)	7	3.30	0.77–4.90	4.70	1.37	2
Witch Hazel (*Hamamelis virginiana* L.)	5	3.25	1.45–6.70	10.15	1.19	2
Hop hornbeam (*Ostrya virginiana* [Mill.] Koch.)	3	2.92	1.07–2.54	6.39	2.21	2
White Ash (*Fraxinus americana* L.)	20	2.45	0.81–3.98	6.58	1.61	2
Red Maple (*Acer rubrum* L.)	24	2.31	0.20–7.30	6.04	1.08	2
Paper Birch (*Betula papyrifera* Marsh)	16	1.79	0.35–5.61	4.18	1.19	2
Sugar Maple (*Acer saccharum* Marsh)	19	1.63	0 –5.04	5.91	1.18	2
Black Birch (*Betula lenta* L.)	11	1.40	0.19–2.40	4.68	1.19	2
Black Cherry (*Prunus serotina* Ehrh.)	7	0.81	0.19–1.66	6.17	2.29	3
Trembling Aspen (*Populus tremuloides* Michx.)	15	0.54	0.04–1.32	6.03	1.68	3
Gray Birch (*Betula populifolia* Marsh)	13	0.53	0.09–1.87	3.93	1.30	3
Large-Toothed Aspen (*Populus grandidendata* Michx.)	10	0.50	0 –1.16	5.03	1.66	3
Beech (*Fagus grandifolia* Ehrh.)	17	0.10	0 –0.75	5.09	0.66	3
R. Oak (*Quercus borealis* Michx. f.)	19	0.02	0 –0.15	3.48	0.97	3
W. Oak (*Quercus alba* L.)	9	0.02	0 –0.07	6.78	1.09	3

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[1] The chestnut leaves were obtained from sprouts.

types but this difference did not stand up when subjected to statistical analysis.

The average palatability of the leaves for the various forest tree species sampled is presented in table IV together with the average percent of ash and the average per cent of calcium. The values given in this table are the average values of all sites from all soil types on which the trees were sampled for the years 1940 and 1941. Table V presents palatabilities of leaves from some trees and shrubs collected from only one soil type. These are subject to considerable error and give only an indication of their relative palatability to millipeds.

TABLE V. *Palatability of leaves for some trees and shrubs collected on one site only*

Species	Sq. Mm. Eaten per Milliped per Night
Witch Hobble (*Viburnum alnifolium* Marsh)	12.30
Alternate leaved dogwood (*Cornus alternifolia* L.)	5.30
Sassafrass (*Sassafrass albidum* Nutt.)	4.60
Beaked Hazelnut (*Corylus rostrata* Ait.)	1.78
Withe-Rod (*Viburnum cassinoides* L.)	0.91
Locust (*Robina Pseudo-Acacia* L.)	0.81
Male berry (*Lyonia ligustrina* L.)	0.67
High bush blueberry (*Vaccinium corymbosum* L.)	0.02
White Pine (*Pinus strobus* L.)	0.00
Hemlock (*Tsuga canadensis* [L.] Carr.)	0.00
Red Spruce (*Picea rubra.* Dietr.)	0.00

The data presented in table IV place the species in order of palatability from the most palatable to the least palatable. Naturally the wide range of values obtained for the palatability of each species make it improbable that the order in tables IV and V is fixed. No doubt any one species might be placed in a somewhat different position had a greater number of trees been sampled for each species, and had the leaves of only one tree been subjected to the millipeds at the same time. The writer feels, however, that the positions given in the tables are approximately correct and would not be changed much on further detailed investigation.

Trials during which the leaves were left in the moisture chamber for several days before adding the millipeds gave an indication that the leaves of a few species might be rendered more palatable by this treatment. Consequently, allowing the leaves to be in the damp container for four or more days before subjecting them to the millipeds might simulate forest floor conditions better.

DISCUSSION

An inspection of table IV shows that the average palatability of the leaves to millipeds is related to the average per cent of calcium in the leaves. The correlation existing between the average palatability of the leaves and the average per cent calcium, as calculated from the data in table IV, is 0.554. This result though highly significant must be accepted with some reservations in view of the fact that the data were not secured from an experiment planned for statistical treatment. However, the conclusion that the palatability of the leaves is related to the calcium content is supported by Chandler's statement (3), "there seems to be a relationship, also, between the palatability of forest tree leaves and the calcium content. . . . That these relationships are entirely concerned with the calcium content of the latter would hardly seem reasonable to suppose. It would seem more probable that the relationship between palatability and leaf type would involve the organic structure of the leaf—that is, the proportion of lignin, cutin, and the like, to the more readily digestible constituents. Nevertheless, a general relationship between calcium content and palatability of the food for soil fauna seems to exist and, therefore, can be used as a guide, regardless of the casual relationship involved."

A study of table IV will show that the data bear out the above statement.

But speckled alder, black cherry, trembling aspen and large-toothed aspen are definitely out of position as regards the relationship between palatability and calcium content. Doubtless, some factor other than the calcium content has influenced the palatability of the leaves of these species and this factor may be one of those suggested by Chandler.

The order of palatability of leaves to millipeds, presented in table IV, has some characteristics in common with the data presented by Johnston ('36) which he obtained as a result of earthworm feeding experiments. One noteworthy exception in the order of table IV, as compared with the order of Johnston, is the position of large-toothed aspen. The palatability of the leaves of this species to millipeds was uniformly low, whereas to earthworms it was quite high in palatability.

The relationship between the average palatability of the leaves and the average per cent ash is not as definite as that between the palatability and the calcium content. The correlation coefficient for the former relationship is 0.496, which is significant but not highly significant.

Chandler ('41) found that the calcium content of the leaves on a percentage basis was not significantly different on the more productive and less productive soils of Central New York. Consequently, the lack of relationship between palatability to millipeds and soil type found in the present study is not surprising. However, the fact that leaves growing on Podzol soils are not less palatable than those growing on Brown-Podzolic soils is interesting in view of the fact that the forest floor tends to accumulate on Podzol soils. The influence of climatic differences on the distribution and prevalence of the fauna of the forest floor may be fully as important from the standpoint of forest floor decomposition as are the differences in vegetation.

For the sake of convenience, the palatabilities of the leaves may be divided arbitrarily into groups. A practical division might be one which divided the species into three groups similar to the one of Chandler's ('39) which was based on calcium contents.

Group 1—Very Palatable Leaves—Those which had over five square millimeters of area eaten per milliped per night.

Group 2—Moderately Palatable Leaves—Those which had between one and five square millimeters of area eaten per milliped per night.

Group 3—Unpalatable Leaves—Those which had between 0–1 square millimeter of area eaten per milliped per night.

These groupings are shown in the last column in table IV. The position of the oaks and the reversed order of sugar and red maple is notable when this grouping is compared to that presented by Chandler ('39).

The practical forester might well keep in mind the palatability of the various species of economic forest trees when he is attempting to improve his stand by selection or by thinning operations. The beneficial effect of mulls on the growth of forest trees is quite widely accepted, and, therefore, it might be wise to aid in the preservation or production of mulls by ensuring a contribution of palatable leaves to the forest floor.

SUMMARY

Millipeds, *Diploiulus londonensis caeruleocinctus* (Wood), become active immediately after the frost in the soil disappears in the spring, but become inactive during July and August. During the latter part of August they suddenly become unusually active and remain active until the soil freezes.

The palatability of leaves from the same tree and from adjacent trees of the same species shows some variability but not enough to mask the difference in palatability between species.

Leaves of some tree species are definitely more palatable than others, and the palatability is correlated closely

with the calcium content of the leaves. In general, the most palatable leaves have a high calcium content while the unpalatable leaves have a low calcium content. Some irregularities occur which may depend on the texture or various organic constituents of the leaves.

The palatability of leaves from different sites on the same soil type exhibits so much variability that soil type differences are not statistically significant, even when representative soil types from both Podzol and Brown-Podzolic great soil groups are compared.

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NOTES AND COMMENT

TRIPOD METHOD OF MAKING CHART QUADRATS

The importance of the chart quadrat is widely recognized. Its use, however, is restricted because it is one of the most time-requiring methods of securing a vegetative record. The making of chart quadrats can be greatly facilitated by the tripod method, which has been used successfully in bunch grass communities.

The following description is of the instrument originally devised and used extensively during the past three seasons (fig. 1). The apparatus consists of a tripod to which a tracing table is attached. An inexpensive, wooden, camera tripod is desirable because of the ease with which a tracing table can be inserted between the legs when they are spread in the ordinary manner. The table consists of a piece of shatter-proof glass 12 inches square, which is supported on a frame constructed from a 1/4 inch steel rod. The frame may be placed between the three tripod legs, at about 1/3 the distance from the apex to the ground, and supported by clamps to each of the legs. The camera attachment screw at the top of the tripod may be removed and the hole enlarged to 5/16 inch for charting work. It may be found desirable to enlarge the hole even more in order that a camera attachment may be added and the quadrat photographed after charting. If the opening is large enough to permit photographing, an eye piece must be added which can be slid into place to reduce the hole to the proper size for charting. The exact size of the opening is unimportant, but it should be large enough to permit an area of desirable size to be examined and yet small enough to prevent undue shifting of eye position.

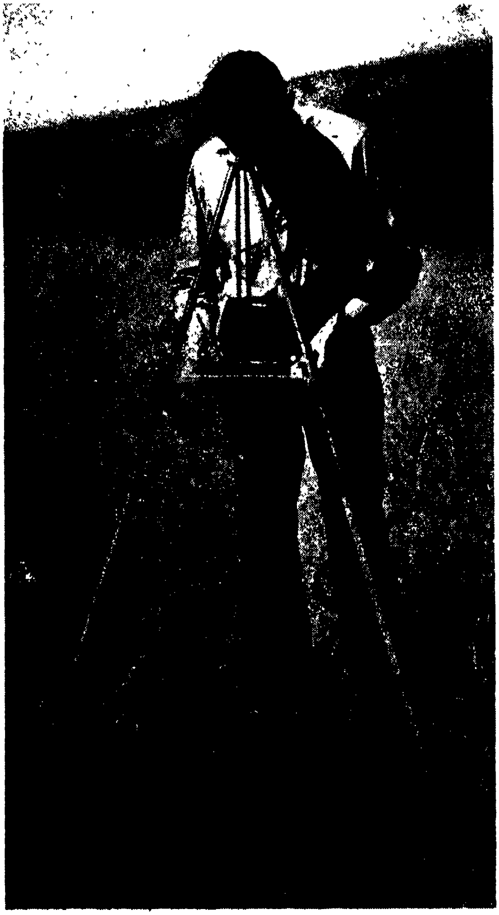

FIG. 1. Mapping a chart quadrat by the tripod method.

The tracing table for most uses is set at a distance of about 15 inches below the eye hole and 30 inches above the ground. The grass should be clipped to a height of about one inch and if small grass seedlings are to be included in the chart it may be found necessary to mark them with toothpicks. Then while looking through the eye hole, the bunches are outlined on cellophane paper or on duPont Plastocele with India ink. If cellophane is used, it should be fastened to the table with pieces of Scotch cellulose tape. Cellophane has the advantage of being more transparent and of being more easily stored since it can be rolled or folded after being used.

A quadrat frame of reduced size made of paper or from a thin metal sheet is placed on the drawing table. The advantage of this small quadrat frame is that it eliminates bulky equipment in the field. A charting area 2½ feet square was found to be a convenient size and was reduced to 10 inches square in plotting. The reduction in size of the drawing can be varied by lowering or raising the tracing table.

This method has been used extensively by the author as a means of checking reconnaissance estimations. The time consumed in setting up the apparatus, charting the bunches of grass, and determining the area by using a planimeter, was found to be a small fraction of that necessary for the use of the pantograph or grated quadrat methods. Another advantage is that only one person is needed for accurate charting, even on what is usually considered as difficult terrain.

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COPPER CONTENT OF SEA WATER

The development of a sodium diethyldithiocarbamate method for determination of small amounts of copper (Callan and Henderson, '29) and the application of this technique to the analysis of sea water (Atkins, '33) stimulated the attempts to determine the exact concentrations in which this metal occurs in the ocean. The problem is of particular interest to those who are engaged in studies of the physiological role of this metal and its accumulation by marine organisms. Since 1933, in connection with my investigations on seasonal fluctuations of iron, copper, manganese, and zinc contents in the tissues of American oysters, I have performed numerous analyses of sea water trying to evaluate the reliability of the carbamate method and to determine the extent of tidal and seasonal fluctuations in the concentration of copper in water.

Attempts to extract copper electrolytically were made in the summer of 1933 using samples collected from the Fisheries Laboratory at Woods Hole; Little Harbor, Woods Hole; and Onset Bay, Massachusetts. Samples of 1 liter of filtered or unfiltered water were heated, stirred, and electrolyzed for 3 to 5 hours; deposits on platinum electrodes were dissolved in normal H_2SO_4 and copper content determined colorimetrically by adding 0.1 per cent carbamate reagent. The strength of the color was read against a standard solution, using a Dubosq colorimeter. Protection of samples against contamination by minute particles of copper from the brushes of an electric motor used for stirring presented considerable difficulties, which, however, were successfully overcome.

During the winter of 1934 and in the following summer numerous analyses were made again at Woods Hole and in Long Island Sound using Atkins' method. Ten ml. of 0.1 per cent carbamate reagent were added to 200 ml. filtered sample, the colored compound extracted with chloroform, and the strength of the color read in a Dubosq colorimeter against a standard solution made up in the same fashion. In other tests the strength of the color was compared with that of the standard using 100 ml. tall Nessler tubes with polished glass bottoms.

In analyzing the samples the utmost care was exercised to avoid contamination. The water used for making reagents was redistilled in Pyrex glassware, and the chloroform was "Bakers Analyzed," redistilled in Pyrex glassware with glass connections throughout. Samples of water were filtered through Whatman's No. 40 filter paper which had been found to be copper-free. The results are summarized in table I.

On August 14, 1942, a series of water samples were collected at half-hour intervals at 20 feet depth (near bottom) at Charles Island, Long Island Sound. The location is of interest because it is one of the sampling stations maintained by the Fisheries Laboratory at Milford, Connecticut, for observations on setting of oysters. The purpose of the test was to determine the extent of variations in the copper content of water in the samples taken between low and high water in Long Island Sound. The results are shown in table II.

TABLE I. *Copper content of sea water from the inshore areas of the Atlantic Ocean*

Date	Source	Method	Cu Content mg./liter
July 7, 1933	Fisheries Lab., Woods Hole	Electrolysis	0.02
Aug. 10, 1933	Onset, Mass.	Electrolysis	0.02
Aug. 11, 1933	Little Harbor, Woods Hole	Electrolysis	0.008
Feb. 15, 1934	Charles Island, Long Island Sound	Electrolysis	0.022
Feb. 15, 1934	Charles Island, Long Island Sound	Electrolysis	0.018
Mar. 1, 1934	Charles Island, Long Island Sound	Electrolysis	0.034
Mar. 17, 1934	Charles Island, Long Island Sound	Atkins	0.03
Mar. 29, 1934	Charles Island, Long Island Sound	Atkins	0.020
May 18, 1934	Mears Creek, Md.	Atkins	0.017
Mar. 17, 1939	Off Providence Island, Bahamas	Atkins	0.001
Mar. 3, 1939	Mastic Cay, Andros Island, Bahamas	Atkins	0.002
Mar. 8, 1939	Loggerhead Creek, Andros Island, Bahamas	Atkins	0.006
Mar. 9, 1939	20 miles WSW of North East Light, Andros Island, Bahamas	Atkins	undetermined
Mar. 23, 1939	Brown Sound, Andros Island, Bahamas	Atkins	0.003–0.008

As one can notice from this table, there was no definite trend in the fluctuation of the copper content within one half of a tidal cycle. It is interesting to note that the copper content near the laboratory dock at Milford Station (mouth of Wepauwaug River) was very high in comparison with that of the water in the Sound. This fact had been reported already by Prytherch ('34) who considers the presence of copper in sea water as one of the factors controlling the attachment of the oyster larvae. This interpretation is disputed, however, by Korringa ('40).

All the samples collected on August 14 had a distinct yellowish coloration similar to that produced by the carbamate reagent. It was therefore necessary to apply a correction which was determined by matching filtered but untreated samples against the standards. In all the instances this correction was high, and in some of the samples it was even equivalent to the reading obtained after the addition of the reagent.

TABLE II. *Copper content of sea water collected at 20 feet depth, near bottom, Long Island Sound, and at the Fisheries Dock, Milford Harbor, August 14, 1942*

Sample Nos.	Time (Eastern Standard)	Tide	Salinity	Color Correction	Copper Content, mg./liter	
					Not Corrected	Corrected
Charles Island						
1	6:50 A.M.	L.W.	26.82	0.020	0.020	0
2	7:20		27.06	0.020	0.024	0.004
3	7:50		27.14	0.020	0.020	0
4	8:20		26.91	0.012	0.024	0.012
5	8:50		27.06	0.024	0.034	0.010
6	9:20		27.40	0.024	0.024	0
7	9:50		27.06	0.024	0.028	0.004
8	10:20		27.32	0.024	0.028	0.004
9	10:50		27.40	0.020	0.028	0.008
10	11:20		27.32	0.020	0.028	0.008
11	11:50		27.20	0.020	0.028	0.008
12	12:20 P.M.		27.06	0.020	0.028	0.008
13	12:50	H.W.	26.91	0.020	0.022	0.002
14	1:20		27.06	0.020	0.021	0.001
Milford						
surf.	9:00 A.M.	2 hrs. fl.	3.94	0.075	0.170	0.095
bottom	9:00 A.M.		26.27	0	0.077	0.077
surf.	3:00 P.M.	2 hrs. ebb	4.38	0.080	0.172	0.092
bottom	3:00 P.M.		25.26	0.024	0.036	0.012

All the analyses so far performed in my laboratory show that the copper content of sea water in the localities studied is very low, rarely exceeding 0.02 mg. per liter. Higher values were observed only in rare instances which represented purely local conditions. In this low concentration of copper, the color produced by the carbamate reagent is too faint for an accurate colorimetric reading and the observed fluctuations may be entirely attributed to experimental error. This was ascertained by making tests with standard solutions of copper salts. Standards made up with greater concentrations of copper could be read accurately, but solutions containing concentrations similar to those found in the sea water were too weak for accurate reading. It was thought that by using a photometer more reliable results could be obtained. A test made with a group of standards of 0.005 mg. of copper in 200 ml. of distilled water gave the following readings, the figures referring to per cent of light transmitted by the colored chloroform solution compared to the amount transmitted by a blank solution: 72.5, 84.3, 84.4, 83.7, 84.0, 68.9, 70.9, 86.7, 88.7. Since this variation of about 20 per cent would mean an error almost as great as the total amount of copper present in the sample, the results are obviously of little value from a quantitative standpoint.

Sodium diethyldithiocarbamate is still the most sensitive reagent for the determination of copper. The amount of copper detectable with this compound may be as low as 0.005 mg. and 0.05 mg. can be determined quantitatively (Mellan, '41, p. 366). The concentration of copper in the sea water is, however, below the lowest concentration capable of an accurate determination.

My experience shows that any process of concentration of the sea water, such as evaporation, involving increased manipulation and prolonged exposure to the atmosphere could hardly be trustworthy because of unavoidable contamination.

The assistance of Mr. Charles Weber, formerly temporary assistant of the U. S. Bureau of Fisheries, and Mr. James B. Engle of the Fisheries Laboratory at Milford, Connecticut, in collecting the samples and participating in analytical work is gratefully acknowledged.

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SALAMANDERS AND SNOW

The male salamander *Ambystoma tigrinum* usually leaves his winter hibernaculum and migrates to water early in the spring before the female. This migration is commonly seen within the breeding range of this species, but rarely do we find them making the trek in snow.

During the week previous to March 15, 1942, while carrying on other biological work at the Valentine National Wildlife Refuge in Nebraska, these amphibians were noted leaving their hibernacula in the sandhills in large numbers and walking to a nearby lake. The migration began during the night of March 11, and was continuing on March 15, when it was necessary to close the observations. By this time, the number in movement was much smaller. Peak of the migration appeared to occur on the night of March 12, but there was no time during the day in the four-day period when they were not seen. The migration occurred along the north border of White Water Lake for a distance of approximately three miles.

A sandhill trail followed the lake shore, and each time the trail was traversed, the number of salamanders crossing it was counted. Counts were made at several hours of the day and once or twice at night. It took fifteen minutes to cover the three-mile trail, and as the salamanders were moving across the trail, it is not believed that the same animal was seen more than once.

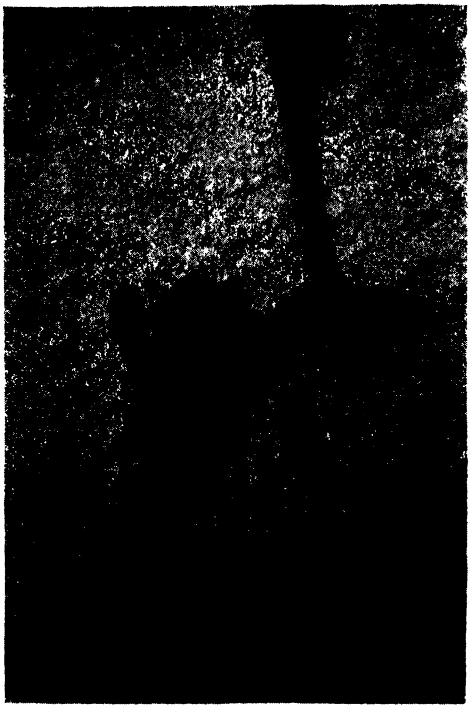

FIG. 1. Tiger salamanders moving over sand

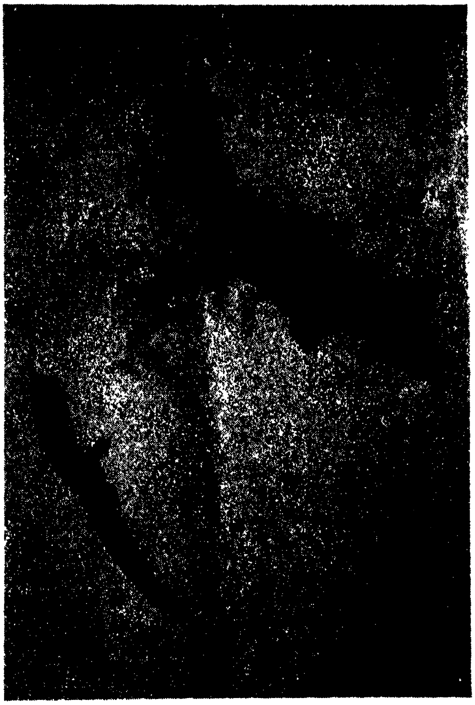

FIG. 2. Tiger salamanders moving in snow

TABLE 1.

Date	3/12	3/13	3/14	3/15
Average temperature	39° F.	42	35	44
Average humidity	88%	82	95	79
Average wind velocity during day. Feet per minute	700	266	700	333
Weather	Cloudy	Cloudy	Cloudy and snow	Partly cloudy to clear
Average number of salamanders seen in migration	66	3	51	14

They moved as though in a hurry, and none was seen walking toward the sandhills, but all were moving toward the water. No females were seen. The average number observed at a given count was 42, and since these were seen in 15-minute periods and there was no evidence that the movement ceased during any hours of the day or night, it is estimated that more than 16,000 of them crawled into the lake during the four-day period.

On the night of March 13, it began to snow and continued to do so all during the fourteenth. Although the temperature was below or just above freezing, the salamanders continued their movement, crawling through the snow like small tanks. As they shoved against it with a slow regular pacing, snow piled up upon their heads until it finally stopped them and they had to shake it off or back away from it. The accompanying figures 1 and 2 show these males moving on sand, then in the snow. Table I lists the weather conditions accompanying this migration and the average number of amphibians seen each day.

With such an abundance of vulnerable prey available, it was expected that predators would move into the region of migration. The only birds seen feeding on the salamanders were crows. They killed and carried away the living salamanders, and also fed upon those which had been killed by automobiles passing along the trail. Coon tracks along the trail indicated the possibility of coons feeding on these.

As this species of salamander is common in the lakes and marshes throughout the sandhills of Nebraska, this estimate of 16,000 males moving into part of one side of one lake gives us some idea of the tremendous numbers involved.

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CRASPEDACUSTA IN OPEN WATER, LAKE QUASSAPAUG, CONNECTICUT

On September 3, 1942, freshwater medusae (*Craspedacusta sowerbyi* Lankester) were found in Lake Quassapaug, six miles west of Waterbury, Connecticut. This is the first indication of their presence in New England. The lake (Riley '37, Deevey '40) covers an area of 271 acres and has a maximum depth of twenty meters. The medusae, approximately 25 in number, were seen swimming in the upper two meters of water in a small area over the deepest part of the lake. One immature individual was captured in a bolting silk townet, the only gear available at the time. After fruitless search in the original locality another group of 40 to 50 medusae was found in an area about 300 meters to the southwest two days later. It is impossible to say whether or not the two groups are identical, but as they are strong swimmers it is not unlikely. The second group was nearer the shore, in water from two to six meters in depth.

Eleven specimens were caught on September 5, all mature males with the distal portion of the gonad greatly elongate. The writers are indebted to Dr. Alexander Petrunkevitch, of the Osborn Zoological Laboratory, for his verification of the sex determination through examination of the sectioned gonads. Two were kept alive and lived for five days in an aquarium. One shed its sperm before dying.

This record is of interest for two reasons. First, in that the medusae were found in open water in a lake of appreciable depth. Most, if not all of the numerous North American localities previously reported are artificial bodies of water, such as concrete pools and standpipes, or else shallow ponds and sluggish streams. The occurrences in Garnet Lake (Von Auken '40), Warren Co., New York, Blue Lake (Causey '38), near Prescott, Arkansas, Sandy Lake (Quick and Matthews '37), Stoneboro Co., Pennsylvania, may also be exceptions. No doubt Craspedacusta is most at home in shallow, plankton rich waters, and our examples presumably drifted across the middle of Lake Quassapaug from northern coves under the influence of the wind. It is almost superfluous to observe that the deep water of Lake Quassapaug has been visited by limnologists dozens of times since 1934, yet medusae have never been seen there before.

The second point of interest is that the known range of Craspedacusta has now been extended slightly to the east. Schmidt's compilation of records in 1939 indicated its presence in 19 states, the easternmost being New York. Since then

Fantham and Porter report Craspedacusta from two places in Canada. Horseshoe Lake, Quebec (approx. lat. 46° N., long. 74.25° W.) is the most northerly record in eastern North America. The second locality is on the Canadian side of the international boundary near Rouse's Point, N. Y. (lat. 44.85° N., long. 73.25° W.). Van Auken's find and Stoner's record for Loudonville, N. Y., together with the Rouse's Point and Lake Quassapaug records (the latter in lat. 41.32° N., long. 73.09° W.), establish the known eastern limit for Craspedacusta as lying between the meridians of 74° and 73° W.

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INDIAN ECOLOGICAL SOCIETY

The Indian Ecological Society was founded at the meeting of the Indian Science Congress at Benares in January 1941. The chief object of the Society is to contribute to a better understanding of the flora and fauna of India by organizing excursions, symposia, popular lectures, etc., and by the publication of information collected by these means. Regional centers are being formed in different parts of India for collecting detailed information on each region. Among the other aims are: mapping of the vegetation of India on modern lines, demonstration of the potentialities of the soil of India, study of phenology, preparation of regional floras and faunas, and promoting the formation of regional herbaria and botanical surveys. The membership at present includes botanists, zoologists, foresters, pedologists, meteorologists, geologists, chemists, geographers, ornithologists, horticulturists and general naturalists. No journal is published, but the Society supplies free to its members, upon request, reprints of articles on Indian ecology published elsewhere by its members. Ordinary membership dues are Rs. 3 per year. Applications for membership and for information may be made to Dr. F. R. Bharucha, Hon. Secretary and Treasurer, Botany Department, Royal Institute of Science, Bombay 1.

FOUNDATION FOR THE STUDY OF CYCLES

In order to stimulate interest in the study of cycles, the Foundation for the Study of Cycles proposes to present a medal to the person making the most valuable contribution to any line of cyclic research during 1943. It is also proposed to award honorable mention for outstanding work along such lines in fields other than that of the winner of the medal. It is hoped that the announcement of these awards in journals of various kinds will help to make people realize how widely the study of cycles enters into diverse sciences such as astronomy, botany, economics, geography, psychology, zoölogy and so on.

Scientific societies are being asked to appoint advisors to cooperate with the Foundation for the Study of Cycles. The advisors will be requested to supply the Foundation with copies of or, at least, references to all articles pertaining to cycles in their fields. This will help to build up a reference library and card catalog for general use at the office of the Foundation in New York. Advisors also will indicate their opinions as to the most valuable contributions of the year to cyclic studies in particular fields. The medallist and the receivers of honorable mention will be chosen from the selections thus made.

Dr. Paul B. Sears, Oberlin College, Oberlin, Ohio has been appointed advisor to represent the Ecological Society of America.

The judges who will award the medal are Dr. C. C. Abbott of the Smithsonian Institution, Professor Wynne Edwards of McGill University, Professor Wesley Mitchell of Columbia University, Dr. Harold E. Anthony of the Museum of Natural History at New York and Professor Ellsworth Huntington of Yale University, Chairman.

Members of the Ecological Society of America who wish to participate in the medal competition will please communicate with the Society advisor, Dr. Sears, or with Dr. Ellsworth Huntington, Hendrie Hall, Yale University, New Haven, Connecticut.

William A. Dreyer, *Secretary*
Ecological Society of America

University of Cincinnati,
Cincinnati, Ohio

BOOK REVIEWS

THE REPRODUCTIVE CAPACITY OF PLANTS[1]

Data gathered during the past 15 years on the reproductive capacity of species and the possible ecological importance of such capacity are presented. The abundance of material, some of it analyzed statistically, adds greatly to the relatively small amount of information previously available. The author makes the broad general summation that "A high reproductive capacity, on the views hitherto orthodox, might be rightly held to be in the nature of a mark of failure, whereas the evidence furnished has shown that a high potential rate of increase is, indeed, rather a criterion of success."

Among many others, the following points are made by the author:

1. The seed or fruit weight tends to augment with the degree of shade to which the seedling is normally subjected. In general, it would appear that the more advanced the phase of succession with which the species is naturally associated the larger the amount of reserve food material provided in the seed.
2. The capacity to colonize in the face of competition appears to be associated with the amount of food reserve which the seed contains.
3. In those species where the variation in seed size is continuous, the experiments by divers investigators would seem to show that the larger seeds confer an initial benefit under conditions of competition.
4. The very great importance of competition as affecting the magnitude of the seed output is demonstrated. Hence the necessity for ascertaining the seed production of species from individuals growing under the natural conditions of their normal environment. This seed output for a particular habitat, as distinct from the far larger potential output in the absence of competition, may be an important factor in determining the occurrence of a species in natural conditions as well as its frequency or abundance.
5. The magnitude of the reproductive capacity appears to bear little if any relation to the risks of mortality, though a certain minimum is obviously necessary to meet those risks, but it would appear probable that, for most species at least, the seed output is considerably in excess of that minimum. The seed output is to be regarded, not so much as an insurance against extinction, as an insurance against rarity, and the effective premium which the organism can afford to pay doubtless bears a definite relation to the available niches in the natural habitats that the plant can occupy.
6. It would seem very doubtful whether the rather large output of seeds is necessitated by mortality risks, as has hitherto been tacitly assumed, but rather that it is advantageous as enabling the species to exploit the special conditions such plants require which often obtain only intermittently.
7. The lowest seed outputs characterize the herbaceous shade species of woodlands, in which the increased pressure of competition and shading to which the germinating seedlings are subject is met by increased seed weight and/or vegetative means of propagation.
8. For most species at least the seed output is considerably in excess of that requisite for mere replacement of losses by death and sufficiently so to bear no obvious relation to the normal seedling mortality.
9. Some of the most successful species are those which exhibit a large seed output and possess also a means of vegetative propagation whilst species in which vegetative propagation is the only or dominant method of reproduction are mostly associated with the more densely populated habitats and the later phases of the plant succession.

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[1] **Salisbury, E. J.** 1942. The reproductive capacity of plants. London: Bell and Sons. xi + 244 pp. 35 figs. 30 shillings.

ECOLOGICAL CROP GEOGRAPHY[1]

This first attempt in textbook form to summarize and integrate the data from a region not adequately explored is a commendable one. It represents over twenty years of thought, and research and teaching in the subject, in a number of agricultural colleges in the United States; and dates back to the author's student days in a course in crop ecology offered by W. L. Burlison at the University of Illinois. That it reflects the author's chief field of interest, agronomy, is probably inevitable. Among plant scientists, agronomists have been most interested in crop ecology, and courses in the general subject are offered in several agronomy departments, this book being the outcome of such a course given by Professor Klages. It will be useful as a textbook chiefly in such courses. While it will serve well as a reference book in courses in ecology, horticulture, geography, economics, or others aiming in the same general direction, the individual crops discussed in detail are primarily those "field crops" considered, in the United States, to lie within the province of the agronomist. Examples in the more general part of the text also are drawn largely from these same plants, so that in some respects the treatment is not as comprehensive, adequate, or well-balanced as the title would imply; and important generalizations that might have been drawn from horticulture are omitted.

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[1] *Klages, K. H. W.* 1942. Ecological crop geography. New York: MacMillan. xviii+615 pp. 108 figs. $4.50.

The author states that the "study of crop ecology should be confined to investigations of the relationships of crop plants to their physiological environments," while the ecological crop geographer considers "the points taken into account by the crop ecologist and in addition must recognize the operation of economic, political, historical, technological, and social forces" (the "social environment"). His book is divided into four parts: The Social Environment of Crop Plants (59 pages); The Physiological Environment of Crop Plants (59 pages); The Ecological Factors (203 pages); and The Geographical Distribution of Crop Plants (254 pages). The first three sections form a background for the discussions of individual crops in Part IV.

Part I is a summary treatment. Although undoubtedly of considerable value in focusing the attention of the agronomy student upon the social factors simultaneously with the ecological factors governing distribution, it is not as well integrated with the discussions in Part IV as are Parts II and III. For this, it is difficult to blame the author, since the differences in the present methods of approach in the diverse fields he attempted to integrate make the task almost superhuman. Part II is a general, simple, and good discussion of habitat and habitat factors, and their general relation to growth and development in plants; physiological limits; crop yields and variability in relation to the ecological optimum; and adaptation. Part III considers the ecological factors of moisture (76 pages), temperature (55 pages), light (17 pages), and air movement (11 pages), from both physiological and climatological standpoints. The treatment of moisture in relation to the whole plant is, in some respects, more adequate than in many ecology and physiology textbooks, while that of light is rather weak. There is a separate chapter on classification of climates which usefully summarizes Köppen's and Thornthwaite's classifications, including their maps for each of the continents; and in Part IV, the author correlates the distribution of many individual crops with the climatic regions outlined in these classifications. A chapter on the edaphic and physiographic factors (15 pages) is the weakest part of the book, as is true in many textbooks of plant geography and ecology. The author attempts to point out only certain general phases, and fails to integrate adequately the intrinsic physiological aspects of these factors with plant function, or to recognize clearly that they can be important regional factors. He follows Schimper, here and elsewhere, in stating that soil factors are local in effect, while climatic factors have regional effects. While all ecologists regard this generalization as more or less true, the point is over-emphasized in this book. Biotic factors are practically ignored, except for incidental mention in the discussion of individual crops. It may thus be seen that the background treatment emphasizes the broad correlations of the geographer, an approach which is often difficult to integrate with the detailed functional approach of the physiological ecologist. It also suggests that possibly the content of courses in crop ecology and ecological crop geography may be limited in part to the integration of those fields not likely to be covered in courses in soils, plant pathology, or economic entomology. Few agricultural colleges have climatologists or geographers on their staffs.

Part IV consists of more or less detailed discussions of the geographical distribution of the small grain crops; the coarse cereals (corn, sorghums, millets); edible legumes (beans, peas, lentils, peanuts); potatoes, sweet potatoes, yams, and other root crops; sugar (sugar cane and sugar beets); oil producing crops (cotton, flax, soybeans, and safflower); fiber crops (cotton, flax, and others); leguminous forage crops (annual, biennial; and perennial); perennial forage grasses; and tobacco, hops, and buckwheat. The discussions vary in length, and in adequacy of the correlation of distributional data with known crop ecology. The assembling of the data included is certainly valuable, but the student of crop ecology will be less satisfied with the treatments given several crops than with comparable discussions in *Climate and Man* (U. S. D. A. Yearbook, 1941). For example, the geographical importance of photoperiod in a crop such as white potatoes is ignored, as are the interacting effects of temperature and photoperiod in bolting versus root production in sugar beets.

The book is pleasing in format, and is well supplied with maps, statistical data, and references, although some of the citations are to out-moded early editions, or to foreign-language works now available in revised English editions. On the whole, in spite of the weaknesses pointed out in this review, most ecologists will be grateful for the writing and publication of this book, and will wish to have it in their own libraries.

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ECOLOGY OF THE OCEAN[1]

In 1855 Commander Matthew Fontaine Maury published his *Physical Geography of the Sea.* The book blazed a new trail and was translated into French, German, Dutch, Norwegian, Spanish, and Italian. This book was chiefly devoted to the ocean as a body of water, little being said of the myriad forms of life that live in it. Since 1855 a vast amount of information has been published on all aspects of the ocean—its tides, currents, waves, chemistry, physics, and, for our interest in this review, its plant and animal life. Much of this information has been accumulated during the past fifteen or twenty years. It is widely scattered and in many languages. What has been urgently needed for some time has been a synthesis of this knowledge, brought together in readily accessible form. It is this synthesis that the authors of "The Oceans" have accomplished, correlating and interrelating the results of published research and vitalizing it all by their own investigations and conceptions, not, however, without caution. "At the risk of premature generalizations we have, however, preferred definite statements to mere enumeration of uncorrelated observations and conflicting interpretations, believing that the treatment selected would be more stimulating."

While providing a mass of factual information the book is specially intended to assist the beginner and the specialist alike in coordinating the various fields of oceanography.

The book has special interest for ecologists. It was more than one hundred years ago (1839) that Edward Forbes pioneered in the study of marine organisms in relation to their environment, and nearly as long ago (1846) that Johannes Müller began the study of the tiny drifting plants and animals to which Hensen in 1887 gave the name plankton. To bring together and analyze the vast literature that has accumulated since then on the myriad forms of ocean life has, of itself been a herculean task, carried out by the authors in a thorough and scholarly manner.

Of a total of twenty chapters, eight are devoted to the plant and animal life of the sea, but of course most of the other chapters are essential for the ecologist giving, as they do, the characteristics of the ocean and ocean water as the abode of life. The headings of what we may call the ecological chapters are as follows: Organisms and the composition of sea water; The sea as a biological environment; Populations of the sea; Observations and collections at sea; Phytoplankton in relation to physical-chemical properties of the environment; Animals in relation to physical-chemical properties of environment; Interrelations of marine organisms; Organic production in the sea.

Each chapter is followed by a copious bibliography. The book will become at once an indispensable item in the library of every ecologist, and every institution where ecology is studied or taught.

C. STUART GAGER

BROOKLYN BOTANIC GARDEN

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[1] **Sverdrup, H. U., Martin W. Johnson, Richard H. Fleming.** 1942. The Oceans: Their Physics, Chemistry, and General Biology. *New York: Prentice-Hall, Inc.* Pp. 1087. 265 figs. $10.00. Text edition, $8.00.

Needham, Joseph. 1942. Biochemistry and morphogenesis. Cambridge: The University Press. Pp. xvi + 787. $12.50. Although this volume is not ecological in any specific sense it is such a comprehensive contribution to biology in general that it deserves a brief descriptive notice in these columns. The modern ecologist, recognizing more-and-more that ecological phenomena merge imperceptibly with many aspects of growth and development, will find that this book contains for him many pertinent data and principles.

Professor Needham is well-known for his "Chemical Embryology" published in 1931. In a sense, the present book is a continuation and extension of that earlier work. This point is adequately made in the Introduction.

"There are three ways in which the great problem of the relation between morphology and biochemistry—the problem to which this book is devoted—can be approached. In the first place we may make a direct attack upon that difficult region lying between the largest chemical particles and the smallest morphological structures which we know. . . . The second way in which we may attempt to bridge the gulf between morphology and biochemistry is by studying the chemical changes which go on during embryonic development, a time during which the morphological change is the most obvious variable. [The third method is] . . . the biochemical investigation of what may truly be called the morphogenetic hormones. The study of these chemical substances, of fundamental importance for all animal and plant development, including its hereditary aspect, occupies the greater part of the present book."

"Biochemistry and morphogenesis" is organized around three major topics: "Part 1. The morphogenetic substratum"; "Part 2. The morphogenetic stimuli," and "Part 3. The morphogenetic mechanisms." The treatment is happily comparative. There is no studied favoritism of vertebrates over invertebrates, or, of plants over animals. Also, morphogenesis in insects is given its share of attention; an aspect frequently overlooked. These features make for scholarship. They are opposed to such cults in embryological thinking (which unfortunately can be duplicated in ecology) as "the amphibian school"; "the chick school"; "the pig school," and so on. The book is documented in excellent style. There are 35 plates either in color or half-tone reproduction as well as numerous pen and ink sketches in the text. In addition, there is a glossary of special terms; a bibliography; a general index; an index of animals; an index of plants, and , interestingly enough, an index of genes. It is our impression that the book is not substantially bound.

This is a welcome addition to biological literature!—T. P.

Fifteen Collected Papers. 1942. The early history of science and learning in America. Proc. Amer. Philosophical Soc., Vol. 86, No. 1. Pp. 204. $1.25 (paper). These are papers read before the American Philosophical Society at its midwinter meeting in February 1942. The papers are not co-ordinated one with the other except in the sense that they deal with interesting personalities in American science. The biological essays are: "Some early botanists of the American Philosophical Society" by M. L. Fernald; "Survey of scientific agriculture" by M. L. Wilson; "A generally overlooked Rafinesque paper" by E. D. Merrill; "Medicine and the American Philosophical Society" by F. M. Packard; "Benjamin Smith Barton as naturalist" by F. W. Pennell; "Entomology, scientific and human aspects" by P. P. Calvert; "The beginnings of vertebrate paleontology in North America" by G. G. Simpson, and "The American indian and the American Philosophical Society" by Clark Wissler. There is a brief introduction by E. G. Conklin. Some interesting reading lies in these pages!

Wright, A. A., and A. H. Wright. 1942. Handbook of frogs and toads. Ithaca, N. Y.: Comstock Publishing Co., Inc. Pp. 286 + 88 photographs. $3.00. The ecologist is always on the lookout for useful taxonomic aids. Here is one on frogs and toads that we recommend for the beginning student. This book is designed ". . . as a guide for teachers, students and even younger naturalists. Of each species, there is a plate of photographs from life and a two-page résumé of its characters and habits. The plates and script are meant to cultivate an interest in the lay mind and help the beginner in his or her quests." The plates are good and should prove useful in making determinations. The taxonomic keys also seem workable. The following data are presented (in most cases) for each form discussed: range; habitat; size; appearance; structure; voice; breeding, and notes.

Rogers, J. Speed. 1942. The crane flies (Tipulidae) of the George Reserve, Michigan. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 53. Pp. 128. $1.25 (paper). This is a monograph of more than usual interest for the ecologist. The crane flies are discussed according to their habitat distribution. There are also some estimates of population size.

Hobbs, Jr., Horton H. 1942. The crayfishes of Florida. University of Florida Publication, Biological Science Series, Vol. 3, No. 2. Pp. 179. $2.25 (paper). Although this is essentially a taxonomic study it should be called to the attention of ecologists because (1) there are many ecological observations about crayfish in the monograph, and (2) crayfish are frequent objects of study by ecologists. There is one section that is particularly ecological and zoögeographical entitled "Factors affecting the distribution of crayfishes in Florida."

Culbertson, James T. 1942. Medical parasitology. N. Y.: Columbia University Press. Pp. 285. $4.25. ECOLOGY consistently calls to the attention of its readers books on parasitology. This is an elementary treatment that ". . . offers a simple and brief description of the animal parasites and the diseases they cause. It is intended as a practical work and deals principally with the epidemiology, pathology, diagnosis, treatment, and prophylaxis of the infections for which the acknowledged human parasites are responsible." Because of the relation of tropical medicine to the war the book is timely. It is not written primarily for the zoölogist.

Allen, R. P. 1942. The roseate spoonbill. Nat. Audubon Soc. Res. Rept. 2: xviii + 142. This work is a study of the past history, abundance, migration, limiting factors, breeding-cycles, food and food habits, plumages and molts, and the future of one of the most beautiful and interesting birds in the Western Hemisphere. It is an admirable example of ecological research. The author spent sixteen months in the field among the mangroves along the shores of the Gulf of Mexico, and nine months in museums, libraries, and laboratories. He gleaned information and took advice from ornithologists, fishermen, old settlers, and ancient writings. He lived for months on lonely Florida Keys. The monograph is well illustrated with drawings, photographs, and a color frontispiece by Roger Tory Peterson. The roseate spoonbill a hundred years ago occupied extensive breeding areas in Florida and Texas, but plume hunters annihilated most of these and only during the last few years has there been reoccupation of a few rookeries. In 1941 there were about the following numbers in the United States: Florida, 513; Louisiana, 150; Texas, 5,035; total, 5,698. Spoonbills migrate north to breeding areas in spring and early summer, and in autumn show less well defined movements. The birds require breeding areas near favorable feeding grounds. They are at times eliminated by high tides, predators (racoons, great-tailed grackles, etc.), and hunters. Birds pair at the beginning of each breeding season. A male brings sticks to his mate who builds a nest; he defends his territory against other males; he takes his turn on the nest two or three times each day. The spoonbill shares its feeding grounds with herons, sandpipers, shoveller ducks, and other animals. Its closest competetors are willets and stilts. Food consists mostly of small fishes, 14–82 per cent; crustaceans, 5–55 per cent; insects 7–31 per cent; gastropods, trace; and plants, 0–3.5 per cent. The six plumages from natal to adult may serve as an index of age.—A. S. PEARSE.

James T. Tanner. 1942. The ivory-billed woodpecker. N. Y. x + 111. Research Bulletin No. 1 of the National Audubon Society discusses the past and present distribution, ecology, life history, and conservation of the ivory-billed woodpecker. It has decreased since much of the timber in swampy forests in the southeastern United States has been cut away by lumbermen. In about five areas in Louisiana and Florida about two dozen individuals were living in 1939. An ivory-bill's food consists largely of wood-boring insect larvae from recently dead trees; and at times of fruits, nuts, seeds, and other vegetable materials. Adults feed mostly in morning and evening. They do not defend definite territories, but return regularly to sleeping holes, sometimes for several years. Eggs are laid from January to May, with an average of 2.9 per nest, and incubation lasts 20 days. Nestings remain in their home hole about 5 weeks, and are fed by parents for two months after that. A single pair of ivory-bills require 2.5–3 sq. mi. of mature swamp forest with plenty of dead trees. The bulletin is well illustrated.—A. S. PEARSE.

Robbins, Wilfred W., Alden S. Crafts, and Richard N. Raynor. 1942. Weed control. xi + 543 pp., 202 figs. New York: McGraw-Hill. $5.00. This comprehensive review stands as the first of its kind in American plant science literature, thus filling a real need as a textbook and manual. Although the primary emphasis is on practical weed-control methods, these are critically discussed and evaluated against the fundamental chemical, physiological, and ecological principles and facts underlying them, and illuminated in many cases by the authors' own experiences. The more recently developed, and hence less well known, chemical methods receive the greatest attention, almost one-half of the text being devoted to a detailed discussion of them, or machinery for application. Among chapters of greatest direct interest to ecologists are: Weeds and human affairs, Reproduction of weeds, Association of weeds with soils and crops, Competition between crop plants and weeds, and Biological control of weeds. There are three chapters on special weed problems of grasslands and turf, cropped areas, and uncropped areas. One chapter is given over to individual discussions of about twenty-five most noxious weeds. The book is well indexed and illustrated, and the typography is of the usual high standard in this series.—C. E. O.

Davis, John H., Jr. 1942. The ecology of the vegetation and topography of the Sand Keys of Florida. Preprinted from Carnegie Institution of Washington Publication 524, pages 113–951. (Papers from Tortugas Laboratory, Volume XXXIII). **Kurz, Herman.** 1942. Florida dunes and scrub, vegetation and geology. 154 pages, 24 plates, 24 figures. Tallahassee, Florida. Department of Conservation, State of Florida. Geological Bulletin No. 23. **Laessle, Albert Middleton.** 1942. The plant communities of the Welaka area; with special reference to correlations between soils and vegetational succession. 143 pages, 14 plates, 25 figures. University of Florida Publication, Biological Science Series Volume IV, Number 1. $1.50. These three papers enrich the details of our knowledge, and may reorient the interpretation, of part of the vegetation of Florida. Each embodies a dynamic point of view, applied with caution and with the recognition of edaphic and other limitations. The first treats of about thirty islands of the Florida Keys, west from Key West and including the Dry Tortugas. Together with the author's earlier paper on mangrove vegetation in Florida (1940, Carnegie Institution of Washington Publication 517), it furnishes a modern and comprehensive account of the vegetation of the coastal and insular region of southern Florida. Vegetation maps of most of the islands are included, that of the principal islands in the Dry Tortugas in great detail. Kurz's paper is a popular presentation which should appeal to citizens of and visitors to Florida, but contains much of scientific interest and soundness. Nine coastal dunes areas are described, seven of the east coast (all but one in the northern half of the peninsula) and two on the northwest Gulf Coast. Their successional relations are emphasized, and the ecological affinities and differences among dune vegetation, "high pine land," and "scrub" are brought out. Laessle's paper is a somewhat detailed account of the vegetation on the University of Florida Conservation Reserve, a tract of 2,180 acres leased to the University in 1939. Besides analyzing associational, edaphic and successional features, it also includes a 28-page chart summarizing the distribution and relative frequency of 750 species of vascular plants among twenty-four natural, seminatural, or distinctly modified habitats, most of them with easily recognized associations.—C. E. O..

Cline, A. C., and S. H. Spurr. 1942. The virgin upland forest of central New England; a study of old growth stands in the Pisgah Mountain section of southwestern New Hampshire. 58 pages, 12 figures. Petersham, Massachusetts. Harvard Forest Bulletin No. 21. This report is based on field studies conducted mostly in 1929–30, and thus provides an analysis which would not now be possible since practically all old growth stands in this region were destroyed in the 1938 hurricane. Stand composition of 68 one-tenth acre sample plots is related to the influence of site, fire, wind, and other natural disturbances. Seven forest cover types are recognized, all developed on podzol soils of the Hermon series. The climatic climax on lower slopes consisted primarily of hemlock, beech, sugar maple, and black birch, while a hemlock-white pine association was the ridge top physiographic climax, with beech, black birch and red maple as minor components. Other associations were mainly pioneer or pre-climax stands in succession following complete or partial disturbance of the climax types. The authors conclude that "the primeval forests, then, did not consist of stagnant stands of immense trees stretching with little change in composition over vast areas. Large trees were common, it is true, and limited areas did support climax stands, but the majority of the stands undoubtedly were in a state of flux resulting from the dynamic action of wind, fire, and other forces of nature. The various successional stages thus brought about, coupled with the effects of elevation, aspect, and other factors of site, made the virgin forest highly variable in composition, density, and form."—C. E. O.

PROCEEDINGS

ECOLOGICAL SOCIETY OF AMERICA, 1942

The New York meeting of the Ecological Society was cancelled on November 27, 1942, following the action of the American Association for the Advancement of Science upon the request of the Office of Defense Transportation.

The program arranged for the meeting was published in the December Bulletin in the usual manner. The election of officers was held by mail. The annual reports of the officers and committees have been received and are printed below. Thus the regular business of the annual meeting has been carried on within the pages of the Society publications.

REPORT OF THE SECRETARY

Membership, December 20, 1941		766
Loss of members, 1942:		
Deceased	3	
Resigned	19	
Dropped, September, 1942	92	
	114	
New members, 1942:		
Associate	5	
Active	26	
Sustaining	7	
Institutional	1	
	39	
Membership, December 5, 1942		691

The principal activity of the Secretary's office this year was the publication of a new directory of membership appearing as Number 2A of Volume 23 of the Society *Bulletin* in September, 1942. In addition to the usual alphabetical and geographical indices and list of officers, a complete and revised list of the standing committees is included.

The 691 members of 1942 include 11 foreign members for whom no mail service is available now and 38 members for whom we have no present address, probably including those who have recently entered the armed forces. The 92 members dropped are those whose names had been carried without payment of dues since 1939 or before and who were omitted, therefore, from the 1942 Directory.

Negotiations with Williams and Wilkins Company resulted in the acquisition by the Society of 646 copies of the *Naturalist's Guide.* According to the plan authorized by the Executive Committee, these books are offered for sale by the Treasurer, as announced in current numbers of the *Bulletin,* and also are placed under the jurisdiction of the Committee on the Preservation of Natural Conditions and the Committee for the Study of Plant and Animal Communities for their use in publicity. The books have been stored in Champaign, Illinois under the jurisdiction of Dr. S. C. Kendeigh, Chairman, Committee for the Study of Plant and Animal Communities. Plans for the complimentary distribution of some of the books by the Committees are now under consideration by the Executive Committee.

Arrangements were made this year by the President, Secretary, and Dr. H. de Forest, Chairman of the Western Section, for the organization of the Committee for the Western Section by election according to the constitutional provision. In view of the expressed approval of this action, it is expected that the procedure will facilitate greatly the functioning of this important division of the Society. Details of the plan and the results of the election are to be found in Dr. de Forest's Report on the Western Section elsewhere in the Proceedings.

Since no complete and revised edition of the Constitution and By-Laws of the Society is available, the President has authorized its publication in the Bulletin. Publication has been delayed by the need for a complete revision of Article VI on publications. Messrs. Pearse and Korstian, Editors of *Ecological Monographs,* prepared a revised form of Article VI which is given below.

Old form.

> Article VI. Publications. The publications of the Society shall be the journal ECOLOGY and such other minor publications, serial or otherwise, as the Executive Committee may authorize. ECOLOGY shall be edited by an Editorial Board, consisting of an Editor-in-Chief, elected by the Society at the same time and in the same manner as the other officers, for a term of three years, and Associate Editors appointed by the Board of Directors for overlapping terms of two years. Active members and Institutional members not in arrears and all Life members shall receive, as issued, the journal ECOLOGY and such other publications as may be designated by the Board of Directors. Associate members shall not receive the journal ECOLOGY, but shall receive announcements of meetings and other minor publications.

New form.

> Article VI. Publications. The publications of the Society shall be the journals ECOLOGY and *Ecological Monographs* and such other publications, serial or otherwise, as the Executive Committee may authorize. ECOLOGY shall be edited by an Editorial Board, con-

sisting of two Editors and twelve Associate Editors, elected by the Society at the same time and in the same manner as the other officers, the Editors for overlapping terms of five years and the Associate Editors for overlapping terms of three years. *Ecological Monographs* shall be edited by an Editorial Board consisting of two Editors and six Associate Editors, elected by the Society at the same time and in the same manner as the other officers, the Editors for overlapping terms of five years and the Associate Editors for overlapping terms of three years. Active members and Institutional members not in arrears and Life members shall receive, as issued, the journal ECOLOGY and such other publications as may be designated by the Executive Committee. Sustaining members and Sustaining Institutional members not in arrears and Sustaining Life members shall receive, as issued, the journals ECOLOGY and *Ecological Monographs* and such other publications as may be designated by the Executive Committee. Associate members shall not receive the journals ECOLOGY and *Ecological Monographs*, but shall receive announcements of meetings and other minor publications. The Editors of ECOLOGY shall be ex officio members of the Editorial Board of *Ecological Monographs*, and the Editors of the latter journal shall be ex officio members of the Editorial Board of ECOLOGY.

Notice of election on this revision was published in the October *Bulletin*. The vote was taken on ballots sent to the members of the Society on February 4, 1943. The opinion of the majority voting within two weeks was considered final. 213 votes were cast for the revision, four against. Therefore, the revision stands approved.

Further preparations are being made now for the publication of the complete constitution and by-laws in the Bulletin.

WILLIAM A. DREYER, *Secretary*
Cincinnati, Ohio
December 20, 1942

REPORT OF THE TREASURER

The Treasurer's Report and reports of other business which is being acted upon by the Executive Committee in lieu of the annual meeting will be published as Part II of the Proceedings in the July, 1943 issue of ECOLOGY.

REPORT OF THE BUSINESS MANAGER FOR THE FISCAL YEAR

DECEMBER 1, 1941–NOVEMBER 30, 1942

RECEIPTS

Cash on hand December 1, 1941		$1,743.44
Dr. Royal E. Shanks, Treasurer E. S. A.		
1 membership 1940	$ 3.00	
28 memberships 1941	84.00	
456 memberships 1942	1,368.00	
21 memberships 1943	63.00	
1 membership 1944	3.00	1,521.00
Subscriptions		
1941 subscriptions	$ 5.26	
1942 subscriptions	1,885.00	
1943 subscriptions	682.54	2,572.80
Advertising		101.00
Back volumes and single numbers		219.65
Authors' Payments		
Excess pages:		
Dr. J. E. Weaver and Irene M. Mueller, July 1942 issue	$ 23.00	
Excess illustrations:		
Dr. E. Schulman, July 1942 issue	8.49	31.49
Miscellaneous		.40
		$6,189.78

DISBURSEMENTS

	Issues	Reprints	
Printing			
Lancaster Press, Inc.			
October 1941		$ 45.01	
January 1942	$1,010.43	36.28	
April 1942	957.49	36.97	
July 1942	1,006.47	29.90	
	$2,974.39	$148.16	$3,122.55

Office Expenses		
Business—Postage	$100.60	
Expressage	2.32	
Stationery	30.64	
Miscellaneous	13.49	
Editorial—Hazel W. Olmsted	8.50	
Mrs. Thomas Park	46.00	201.55
Advertising		40.69
Office Assistance		
Accounting Service—December–November	$120.00	
Mary E. Sturtevant—Secretarial serv. to Ed.	10.00	
Evelyn M. Kostanski—Secretarial serv. to Ed.	12.50	142.50
Miscellaneous		
Purchase of back volumes	$ 7.00	
Auditing of books for last fiscal year	5.00	
Refunds of subscriptions	14.65	
Payments made as subscriptions, should have gone to "Ecological Society" for membership	15.05	
Exchange charge on money order	.10	
Refund on advertisement	8.00	
Reimbursement for cablegram	1.13	50.93

TOTAL DISBURSEMENTS	$3,558.22
BALANCE November 30, 1942	$2,631.56
	$6,189.78

Examined and found correct, December 21, 1942.

H. P. SCHOENBERNER, *Auditor*

BALANCE SHEET—NOVEMBER 30, 1942

Assets

Cash in bank		$2,631.56
Accounts Receivable		
Single numbers	$4.50	4.50
		$2,636.06

Liabilities and Working Fund

Bills Payable	
Lancaster Press, Inc.—October issue	931.97
Working fund (assets over liabilities)	1,704.09
Total liabilities and working fund	$2,636.06

Circulation data as per mailing-list for the October issue:

1. Members of the Ecological Society		
U. S. A.	461	
Foreign	25	486

2. Subscribers			
U. S. A. individual subscribers	3		
U. S. A. institutional subscribers	325	328	
Foreign individual subscribers	6		
Foreign institutional subscribers	82	88	
3. Advertisers		11	
4. Exchanges			
Domestic	11		
Foreign	25	36	
5. Editorial		2	951
Number of copies ordered printed for January and April			1500
Number of copies ordered printed for July and October			1450

C. Stuart Gager, *Business Manager*

Report of the Editors of Ecology

Volume 23 (1942) of Ecology contained 500 pages as compared with the 472 pages of Volume 22 (1941). We have sufficient accepted manuscripts in both animal and plant ecology to run into the July 1943 issue. We are not yet sure about the effect of the war on either the number or the quality of manuscripts submitted. The 1943 Editors' report should answer this question.

We wish to thank the Editorial Board and other consultants for their generous assistance. Their skilled and critical treatment of manuscripts has been invaluable to us in reaching our editorial decisions. Also, our thanks are due to Dr. C. Stuart Gager who, as Business Manager of Ecology, has been both helpful and cooperative in the effective running of the journal.

The Editors wish to register their keen sense of loss at the passing of Francis Ramaley in June 1942. As former Botanical Editor he was our friend and cordial consultant. We shall miss him!

Respectfully submitted,
Thomas Park
Charles E. Olmsted

Report of the Editors of Ecological Monographs

On behalf of Exie Duncan, Business Manager of *Ecological Monographs*, we submit the following statement:

Paid subscriptions	227
Paid by Duke University Library for exchanges	37
Free and exchange	21
Total circulation	285

For year ending July 1, 1942

Income	$2,629.29
Expenses	4,643.31
Expenses over income	$2,014.02

A. S. Pearse
C. F. Korstian

Report of the Committee for the Western Section, Ecological Society of America

The Western Section of the Ecological Society of America participated in the Salt Lake City meeting of the American Association for the Advancement of Science June 15–20, 1942. The Ecological Society took part in two joint sessions. One was held with the Western Society of Naturalists, for a symposium on "Salinity as an Ecological Factor." In this there were four speakers, three from the University of Utah and one from the University of Nevada, all provided by the Ecological Society. The other joint session was held with the Pacific Division of the Botanical Society of America. Seven papers were presented upon a variety of botanical and some zoological subjects. Three of the speakers were provided by the Ecological Society, two from California and one from Montana. The official program of the American Association for the Advancement of Science was unaccountably in error in a few particulars of the Ecological Society program. It is understood that all the field excursions on the official program were abandoned at the last moment.

Because of the war most of the Salt Lake City sessions were rather poorly attended. Some criticism has been heard of poor preparation of papers and poor delivery throughout this AAAS meeting. One of the seven Ecological Society papers has been specially commended for careful preparation and excellent delivery. Another paper was given by someone who had been ill and who really did well to appear at all in order not to disrupt the program. The other five Ecological Society papers probably ran as high in quality and delivery as did the papers of other organizations. Perhaps the war situation has brought about some lowering of the quality of scientific papers at such meetings.

Instead of the President of the Society appointing a Committee for the Western Section, this year the plan of electing the committee, as is provided for in the Constitution and By-Laws, was followed. It undoubtedly meets with the approval of the western membership, most of whom have expressed themselves in favor of this means of obtaining their committees.

A Nominating Committee composed of Messrs. Walter P. Cottam, University of Utah, Kenneth L. Gordon, Oregon State College, and Arthur W. Sampson, University of California, was chosen by the Committee for the Western Section, 1942. This committee selected about fifteen nominees and from these a slate of eight was obtained. From these eight, three committeemen were elected, to serve for the two-year period 1943–44. The nominee who received the greatest number of votes, irrespective of the number cast, became Chairman of the committee for 1943, and the nominee receiving the next greatest number of votes became Chairman for 1944. It developed that the ballot cast, even after an extension of the time, was exceedingly close for a few of the proposed committeemen. Upon appeal to President Korstian, it was decided that a second vote should be taken for two of the three committeemen. This was carried out and the final result was as follows: H. de Forest (Botany), University of Southern California, Chairman, 1943. Tracy I. Storer (Zoology), College of Agriculture, University of California, Chairman, 1944. Thornton T. Munger (Forestry), Forest Service, U. S. D. A., Portland, Oregon, committee member.

The Chairman of the 1942 Committee feels constrained to comment upon the lack of mention of the Western Section of the Society in the Proceedings of the Society as published in ECOLOGY, April, 1942. On account of the important contributions of the Western Section to the meeting of that year, 1941, held at Pasadena, California, brief mention is made of them here. Two symposia were organized by the Committee for the Western Section, 1941. These symposia were listed in the official program as joint symposia with the Western Society of Naturalists and the Society of American Foresters. Neither of these organizations was able to assist. The papers of the symposium, "Ecological Aspects of Evolution," appeared in full in *The American Naturalist* of January-February, 1942, volume 76, number 762. Those of the symposium, "The Development of Quantitative and Experimental Work in Ecology," also in full, appeared in ECOLOGY as a bound-in supplement to the October, 1941 issue, volume 22, number 4. A critical discussion of the former symposium was published in *Chronica Botanica* during the summer of 1942.

A financial statement of the Committee for the Western Section, Ecological Society of America, for 1942 was presented to the President and the Treasurer of the Society and was accepted as satisfactory.

H. DE FOREST, *Chairman*

Los Angeles, California
December 31, 1942

REPORT OF THE COMMITTEE ON THE PRESERVATION OF NATURAL CONDITIONS IN THE UNITED STATES

Conditions arising from the war have raised numerous questions of policy and use in connection with the protection of national parks and other preserves. Funds for adequate protection of natural areas and also for the study of wildlife have been endangered. This Committee has attempted to gain information on these problems and, in certain instances, taken action in accordance with the long-established objectives of the Society.

The Committee has suffered a great loss through the passing of Dr. Francis Ramaley, whose service to Ecology will be long remembered.

During 1941 and 1942, the Tularosa Malpais, in New Mexico, has been the subject of considerable interest, and a subcommittee has considered the area as a possible addition to the White Sands National Monument. Following a conference between members of the War Department and the Department of the Interior, a bombing range was established in the Tularosa Basin—an action made necessary by the war. The range is located north of the White Sands and does not include any part of the monument. Reportedly, the lava beds within the bombing range will not be disturbed very much. It is believed that chances are good for getting a portion of this area set aside at the conclusion of the war, and consideration should be given now to the desirability of a resolution aiming to have it made a part of the White Sands National Monument.

Public Contact committee members from Pennsylvania, Mrs. J. F. Stanwell-Fletcher and Mr. F. R. Cope, Jr., have reported on the Kitchen Creek Virgin Forest Area and the Silver Lake Virgin Forest area. The former contains about 1200 acres and the latter 800 acres of fine virgin hemlock-hardwood forest. These areas are now in danger and it is our opinion that action should be taken now by the Society in the form of a resolution to give support toward having these two tracts of virgin forest in Northeastern Pennsylvania preserved in their natural condition.

The Committee for the Study of Animal and Plant Communities has investigated the need for having the Porcupine Mountain region in Northern Michigan established as a Natural Area, and the South Calaveras Sequoia Grove in California, likewise, preserved by having it included in the nearby Big Trees State Park. On a basis of the findings of the Study Committee it is desirable for the Committee to have a resolution passed by the Society favoring action toward the protection of the South Calaveras Sequoia Grove.

The war has made it necessary for parts of certain state parks to be taken over for temporary or permanent use. There is considerable pressure on the Olympic Peninsula in Washington for Sitka spruce, used in the construction of airplanes. However, reports indicate that as yet little damage has been done.

During the year, the Committee campaigned in the interest of securing adequate congressional appropriations for protection against forest fires and for the provision of adequate funds for continuing essential wildlife research. In the Sixth Supplemental National Defense Appropriation Bill for 1942, five million dollars was designated for forest fire control. This measure was passed by the House and Senate and approved by the President on April 28, 1942.

Work on the provision of a revised and extended list of persons serving on the Public Contact Committee and of conservation organizations affiliated with the Society has been continued. Reprints and mimeographed copies of several articles provided by the Study Committee have been purchased and distributed to all members of the Public Contact Committee and to as many conservation organizations as the supply permitted. Efforts are being made to establish more frequent and closer contacts with these individuals and organizations, so as to provide a more responsive unit with greater functioning power when campaigns are undertaken.

This Committee wishes to thank all those who have assisted in its work during the year. It is hoped that members of the Society will continue to advise this office of any situations coming to their attention that need our consideration.

The treasurer's record of disbursements for the Committee during the year are:

July 25, Clerical work	$28.00
July 25 and October 16, Reprints	21.95
Total	$49.95

The Committee requests that its annual allocation by the Society of $50.00 be continued.

Respectfully submitted,
CURTIS L. NEWCOMBE, *Chairman*
Williamsburg, Virginia
December 21, 1942

REPORT OF THE COMMITTEE ON THE PRESERVATION OF NATURAL CONDITIONS FOR CANADA AND NEWFOUNDLAND

During the year the Committee has cooperated with the Committee for the Study of Plant and Animal Communities by supplying information on parks and other reserves of natural areas in Canada.

Special attention has been given to the possible effect of the Canadian-Alaskan highway on natural conditions in areas through which this highway passes. There are no detailed maps of the area and no biological surveys have been made on the regions traversed. Our committee, however, fearing that access to regions through which the highway passes might lead to the destruction of natural conditions in areas of outstanding value from the ecological and recreational points of view made representations to Hon. T. A. Crerar, Minister of Mines and Resources, suggesting that steps be taken to reserve areas of surpassing value. In reply Hon. Mr. Crerar has informed us that an officer of his department has acted as liaison officer between departments of the Dominion Government and United States authorities on the highway since the beginning of June this year. He lived and travelled along the highway studying conditions as they relate to conservation. Along that part of the highway situated in Yukon Territory all unalienated lands within a distance of one mile each side of the highway have been reserved from entry or disposal except under special permit. The principal object of this precaution is to ensure orderly and desirable development of areas adjacent to the highway.

Action is also being taken to withdraw from entry or disposal a tract of land containing some 10,130 square miles adjoining the highway in southwest Yukon Territory, between Kluane Lake and the international boundary, in order that it may be available for national parks purposes. This area includes a great deal of mountain and glacier scenery of superlative excellence, as well as lower lands with a large population of big game mammals, and will, undoubtedly, form an outstanding national park, but it is unlikely that it will actually become a national park until after the conclusion of the present war.

Part of the area adjacent to the highway in the Northwest Territories forms part of the Mackenzie Mountains Preserve, in which hunting and trapping is restricted to the native population and to the few white men who were trapping in the area prior to the establishment of the preserve. Part of this area may later be constituted a national park. In the meantime the present status perhaps affords reasonable protection for wildlife.

The original Quebec and Newfoundland representatives on our Committee have resigned. I therefore ask that their places be filled by the appointment of Dr. Georges Maheux, Department of Agriculture, Quebec, P. Q. and Dr. Wilfred Templeman, Memorial University College, St. John's, Newfoundland.

J. R. DYMOND, *Chairman*

REPORT OF THE COMMITTEE ON APPLIED ECOLOGY

No report.

JOHN M. AIKMAN, *Chairman*

REPORT OF THE COMMITTEE FOR THE STUDY OF PLANT AND ANIMAL COMMUNITIES

The work of this committee during the past year has been concerned with compiling additional information for the inventory of nature sanctuaries in North America and in collecting information about new areas that should be preserved.

The inventory includes over five hundred areas that are already preserved in some form. Although the names of several new areas were added tp the inventory this past year, we have now reached the point where all the more important sanctuaries in North America have probably been listed at least by name. The task remains of acquiring sufficient descriptive material on each area in order to classify it to its ecological type, degree of disturbance from original primitive conditions, and general adequateness. We have prepared in mimeographed form a classification to the biomes where they belong of approximately half of the areas, concerning which there was more information. Copies of this list are available on request.

Publications sponsored in whole or in part by this committee during the year have been: Research areas in the National Parks, January 1942, ECOLOGY, **23**, 1942: 236–238; and Biological control of rodents and predators (by V. E. Shelford), *Scientific Monthly*, **55**, 1942: 331–341. The organization of the committee was brought up to date and its complete membership was published in the new directory: *Bull. Ecol. Soc. America*, **23**, 1942: 26–30. Reprints of these articles have been mailed to all committee members and are available to others who wish them.

The Ecological Society will need to continue its vigilance over natural areas even after they have been legally set aside in an enduring and satisfactory manner. This vigilance must be attentive not only to disturbance from human intrusion but also to changes in the relations of the constituent plants and animals involved in the communities. We have long been concerned with reports of over-grazing and over-browsing by the large ungulates in such areas and these reports have recently indicated such serious disturbances that original natural conditions are no longer represented. Perhaps this has been due in large part to reduction or elimination of the larger predators which allowed a break-down in the natural balance between plant food, ungulates, and carnivores. In the larger natural areas normal conditions might be restored by allowing the predators to return to former numbers, but this is not easily accomplished in the smaller areas, and other maintenance or restorative policies must be worked out. A subcommittee has been organized to study this problem, to gather together all available information, and to make recommendations as to policy.

The committee is keeping in touch with movements to preserve natural areas in the Singer Wildlife Refuge area in Louisiana, the Porcupine Mountain area in Michigan, the South Calaveras Sequoia Grove in California, the Tulerosa lava bed in New Mexico, prairie areas in Missouri, the Kitchen Creek and Silver Lake Virgin Forests in Pennsylvania, Dismal Swamp in Virginia, as well as other smaller areas. War conditions hinder rapid advance in getting them set aside for preservation, but a watch will be maintained for opportunities in which the Ecological Society may exert its influence in the proper manner.

Expenses for the work of the committee during the past fiscal year have been as follows:

Stenographer	$52.40
Mimeographing	6.84
Express charges	1.52
Postage	6.63
Reprints	15.73
Total	$83.12

Unexpended appropriations from previous years will take care of the amount above fifty dollars which was assigned to the committee at the last business meeting in 1941. The chairman recommends that fifty dollars be again allocated to the committee for the coming year.

Respectfully submitted,
S. CHARLES KENDEIGH, *Chairman*

REPORT OF THE COMMITTEE ON NOMENCLATURE

The committee held two meetings at Dallas in connection with the program of the Society in that city during December, 1941. A report of some length (ECOLOGY, **23** [2]: 255–257), which reviewed the history and work of the committee since its formation in 1931, was presented at the business meeting held on the afternoon of December 31.

During the past year, the committee has been especially active, although by reason of the wide geographical separation of its members, all business has had to be transacted by mail. Work on the fourth list of definitions has been pushed forward and each member of the committee has contributed to the effort.

Since the Dallas meetings, new and separate lists of terms have been submitted by the chairman to each member of the committee for new definitions or for any needed revision of old definitions. As fast as these lists of definitions have been sent back to the chairman, they have been duplicated and mailed to each other member of the committee for criticism and possible further revision. In this way, the work of each committee member is being reviewed and criticized by all other members. We hope to improve materially the quality of the definitions by this method.

Each committeeman has also been requested to submit additional ecological terms which he feels should be included in the final form of the fourth list. Most of the men have sent suggestions to the chairman and he has assigned these new terms to various members of the committee for definition. Some of these second lists have been returned and one of them has subsequently been duplicated and copies mailed to each person on the committee. Once again we urgently request all interested members of the Society to send to the chairman of the committee lists of terms which they feel the committee should include in the next list.

As mentioned in the report of last year, the Society appropriated fifty dollars in 1940 to help defray the expenses of the committee. Approximately half of that sum has been expended thus far, largely for postage and for clerical and stenographic help in connection with preparation of the various lists in the office of the chairman.

The committee requests that the present personnel be continued and that any unexpended sum remaining from the original appropriation at the close of the fiscal year on December 1, 1942, be made available for use of the committee to help defray its expenses during 1943.

Respectfully submitted,
FRANK E. EGGLETON, *Chairman*

SIXTH REPORT OF THE COMMITTEE ON A REPOSITORY FOR THE HISTORICAL RECORDS OF THE ECOLOGICAL SOCIETY OF AMERICA

During this year the Committee has continued to study the problem of finding a suitable repository for the historical records of the Society, and, at the suggestion of Dr. Fuller, has considered the library of the University of Cincinnati. A preliminary survey indicates that this location would fulfill the requirements previously set forth by the Committee (ECOLOGY, 22: 226, April, 1941) and has the endorsement of the President and Secretary of the Society.

Plans are being made now for assembling the material to be deposited and for formal negotiations with the University of Cincinnati Library. Therefore, the committee recommends that it be continued.

GEORGE D. FULLER
ROBERT F. GRIGGS
CHAS. C. ADAMS, *Chairman*

REPORT OF THE COMMITTEE ON QUANTITATIVE ECOLOGY

The year was a difficult one. In particular, a projected Christmas meeting with the Biometrics Section of the American Statistical Association, on the problem of Optimum Catch, proved impossible. It is hoped that the committee will be continued and may undertake this session at a later date.

Respectfully submitted,
W. C. ALLEE
STANLEY A. CAIN
THOMAS PARK
GEOFFREY BEALL, *Chairman*

REPORT OF THE NOMINATING COMMITTEE

The Nominating Committee makes the following recommendations to the Ecological Society of America:

For *President:* Orlando Park
For *Vice-President:* Paul B. Sears
For *Treasurer*, 1 year, replacing Royal E. Shanks: Stanley A. Cain
For *Committee Member of Executive Committee:* S. C. Kendeigh
For *Botanical Editor, Ecological Monographs*, 5 year term: C. F. Korstian
For *Editorial Board*, ECOLOGY, 3 year terms,
  in botanical field: Wm. G. McGinnies
  in botanical field: R. S. Campbell
  in zoological field: Paul S. Welch
  in zoological field: Harry S. Smith
For *Editorial Board*, ECOLOGY, 2 years, replacing H. I. Baldwin: H. J. Lutz
For *Editorial Board, Ecological Monographs*, 3 year terms,
  in botanical field: A. W. Sampson
  in zoological field: W. P. Taylor
For *Representative, Union of American Biological Societies:* Robert F. Griggs
For *Chairman, Committee on Applied Ecology*, 3 year term: John M. Aikman
For *Chairman, Committee for the Study of Plant and Animal Communities*, 3 year term: S. C. Kendeigh

The Nominating Committee understands that Professor Newcombe was elected Chairman of the Committee on the Preservation of Natural Conditions for the United States two years ago and that his term, therefore, continues during the coming year.

The Committee recommends that in the future the date of expiration of the term of each official, where the officer is elected for a term of more than one year, be designated in the report of the Nominating Committee as published in the Proceedings of the Society and be indicated in the published list of officers and committee chairmen as is done now in some cases but not in all.

Respectfully submitted,
J. E. WEAVER
CHAS. T. VORHIES
R. E. COKER, *Chairman*

The report of the Nominating Committee was submitted to the members of the Society for election by mail on February 4, 1943. The opinion of the majority voting within two weeks was taken as final. 219 votes were cast for the ballot as given above. 11 votes were cast against a few of the nominees but not more than two against a single individual. Therefore, the officers nominated stand elect.

William A. Dreyer, *Secretary*

21 SEP 1955

ECOLOGY

VOL. 24 JULY, 1943 No. 3

OBSERVATIONS ON THE ECOLOGY AND NATURAL HISTORY OF ANURA IV. THE ECOLOGICAL DISTRIBUTION OF TOADS IN OKLAHOMA[1]

ARTHUR N. BRAGG AND CHARLES CLINTON SMITH

INTRODUCTION

It is rare to find ecological factors stressed in papers dealing with the lives of frogs and toads. On the one hand, herpetologists (with some exceptions) have emphasized taxonomy, geographical distribution, and habits of various groups; on the other, ecologists have commonly regarded these animals as of only minor significance in the communities of which they are a part and, therefore, have mentioned them only incidently, if at all.

In the earlier papers of this series (Bragg, '40, '40a, '40c) it has been shown that in Oklahoma various species of Anura are segregated in ecological areas and that their habits are such as to fit them nicely into various ecological niches. Even closely related species differ thus in habits; and some of them have habit patterns so firmly fixed in their hereditary constitutions that this alone serves as a very effective barrier to their dispersal. Also, some species, more flexible than others, are able to change their habit pattern to meet different environmental conditions and, therefore, to have a wider dispersal, both geographically and ecologically, than other closely related species. Further evidence of these relations to environment has recently been found in New Mexico (Bragg, '41) and some of the breeding patterns in Oklahoma have been related to cytological, physiological, and other, environmental, factors (Bragg, '41a, '42a).

During the earlier phases of this study, it became evident that terrestrial and fossorial species especially may play an important part in the communities known as grasslands. Toads of the genus Bufo, for example, feed almost exclusively upon arthropods, and, of these, the ground-dwelling nocturnal insects form a large percentage (Smith and Bragg, '42). Toads are not only largely nocturnal but also they often occur in enormous populations in the grassland biome (as defined by Carpenter, '40). No accurate census of toads has been made but we have consertively estimated populations exceeding one thousand per acre in several portions of the mixed grass prairie of Oklahoma; numbers, moreover, which cannot fail to have profound effects in the whole series of complex successions involved.

Because of these considerations resulting largely from the work of the senior author, it seemed wise to study the whole assemblage of Anura in Oklahoma from an ecological viewpoint and, to this end, the junior author joined the work. Together or individually with coworkers we have collected and studied in all parts of Oklahoma, including from one to several visits to each of the seventy-seven counties. Central and southwestern regions have been most adequately covered in the collection of Amphibia.

The present paper presents our data

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[1] Contribution from the Zoölogical Laboratory of the University of Oklahoma, No. 213. Aided by a grant to the senior author from the Faculty Research Fund of the University.

and conclusions concerning the genus Bufo. Other genera will be reported upon later. We have collected well over three thousand specimens of Bufo in Oklahoma, in every case accompanied by careful observations upon the ecological conditions present. Extensive notes on breeding habits, breeding sites, etc. together with broader ecological observations have guided us in our interpretations of ecological distribution.

In addition, we have had access to all specimens in the Museum of Zoölogy of the University of Oklahoma and to the field notes of the University of Oklahoma Biological Survey. Altogether, we have examined well over five thousand specimens and have observed uncountable numbers in breeding congresses in all parts of the state. Our field observations were made in the spring, summer, and autumn of 1939 and 1940 and in the spring and summer of 1941.

We have found it necessary to study our subject from the following points of view: (1) to map carefully the ecological associations of Oklahoma, (2) to correlate the distributional records of toads with these, (3) to correlate the habits of the various species with their ecological distribution, and (4) to correlate our findings with those of other workers in adjacent regions, principally Texas, Kansas and Arkansas. We have confined most of our personal observations to Oklahoma, although we have made a few trips to adjacent regions of Arkansas and Texas and the junior author made some observations in Louisiana.

Identification of specimens of toads in Oklahoma is, for the most part, easy. However, the specimens from the eastern part of the state offer certain difficulties, as is explained in the discussion. In order that others may check our identifications, all of our specimens have been deposited in the Museum of Zoology, University of Oklahoma, with the exception of a few which have been retained for our own collection.

ACKNOWLEDGMENTS

We are indebted to Dr. A. I. Ortenburger for use of specimens and records under his care as well as for suggestions and criticisms concerning the strictly herpetological phases of the work, to Dr. A. O. Weese for suggestions regarding the ecological phases of the study, and to the graduate students who accompanied the authors on the numerous field expeditions. We also wish to thank Professor George A. Moore of the Oklahoma A. & M. College and Professor H. D. Chase of the University of Tulsa for permitting us to examine specimens in their collections and to report several new county records from these specimens.

ECOLOGICAL ASSOCIATIONS OF OKLAHOMA AND ADJACENT STATES

The ecological communities in Oklahoma have never been studied adequately although the vegetation of the area was mapped by Bruner ('31) as correctly as the data then available permitted. We have found it necessary to study this matter in some detail in order to determine how the various species of toads are distributed within each association represented in the state. Certain of the boundaries between regions as indicated by Bruner have been changed by us due to additional knowledge. Since most of the major communities overlap into adjacent states and the toads apparently follow them, we have included in our map (figure 1) the vegetation of some of these adjacent areas. For this purpose, we have relied mostly upon the works of Bray ('01) and of Tharp ('26) in Texas and of Gates ('36) and of Albertson ('37) in Kansas, supplemented by more limited observations of our own, particularly in northern and western Texas.

To us, ecological associations are not synonymous with "plant associations;" but we do agree with those who believe that the prominent or dominant vegetation gives a good basis for naming the larger communities, as well as the seral

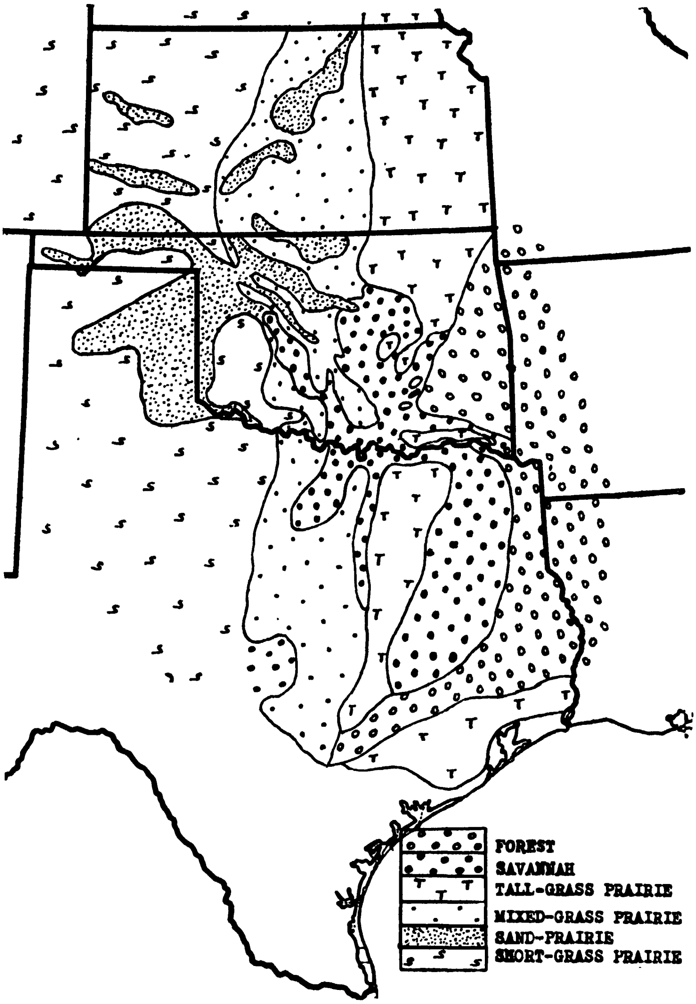

FIG. 1. Plant associations in Oklahoma and adjacent states.

stages in succession. This should be clearly understood in considering all ecological phases of this paper. Toads are distributed with certain plants, not because they depend upon the plants, but because both depend upon climate, amount of available moisture, interrelations of these with other factors and with each other in exceedingly complex ways. In other words, both the toads and the plants are parts of a *biotic* community from which they receive sustenance and to which they, in turn, contribute. Since various types of prairie, woodland, or savannah differing floristically also show corresponding differences, faunistically, it is possible also to use the plants in naming ecological subdivisions. In order to correlate the distribution of toads with the biotic communities of which they are a part, therefore, it is necessary to give the flora of these subdivisions in some detail.

In Oklahoma we find these associations represented; Oak-Hickory forest in the eastern one-sixth of the state; Oak-Hickory-Andropogon savannah in the east-central part; Mixed-Grass prairie in the west-central portion; Short-Grass prairie in portions of the extreme west and southwest and Tall-Grass prairie in the northeast central portion of the state. Along the major streams in the western half of Oklahoma and also in regions occupying considerable area away from the streams in the extreme west is a bunch-grass sand-prairie association. This has not been accurately mapped and we have not found it possible to map it with the limited data at hand.

Quercus-Hicoria Association, Quercus-Hicoria-Andropogon (Savannah) Association

The woodland area of Oklahoma is extensive and composed of several different types. The south-central part of the state is covered with an open woodland in which *Quercus marilandica* and *Q. stellata* are dominant and in which Hicoria spp. were formerly abundant. This woodland is for the most part quite open and much of the ground is covered with grasses, chiefly *Andropogon scoparius,* with *A. ternarius* common. Various legumes are also present. The western boundary of this association in Oklahoma extends from western Payne to central Logan county then south through Cleveland and McClain, eastward into Pontotoc county, then southwestward across northern Love county, and southward to the Red River (figure 1). In Texas the same association extends from the Brazos river in Waller, Brazos and Robertson counties north and east to the Red River (Eastern Cross Timbers) and along the Red River west to Wichita county with an extension southward along the 97th meridian to central McLennan county (Central Cross Timbers) and another in Montague county southwest to Jacks county (Western Cross Timbers). The Western Cross Timbers are represented in Oklahoma by an area in Love, Carter, Stephens, Grady and Caddo counties. The main savannah area in Oklahoma lies between the mixed-grass association along its western edge and the oak-hickory forest on the east. The northern end of the area joins the true prairie in northern Oklahoma.

The southeast corner of Oklahoma (LeFlore, Latimer, Pittsburg, McCurtain and Pushmataha counties) includes part of the Ouachita uplift and is covered with a mesophytic eastern-deciduous-forest type of vegetation on northern slopes and in moist valleys, oak-hickory-grass on the dry ridges, and woodland on the south slopes. Immature soils formerly supported stands of pine (*Pinus echinata*). Pine also occurs scattered throughout the oak woodland. The Ozark uplift extends into northeastern Oklahoma and is covered with oak-hickory forest in which also scattered pines are found.

The oak-hickory savannah is of particular interest because it lies in a region which, climatically, would be expected to have a prairie climax. Because of the sandy character of the soil, water is readily absorbed during periods of precipitation and readily given up to plants over a long period of time. These conditions favor woody species, such as oaks and hickories, which can utilize the water from the deeper soil horizons that is not available to more shallow-rooted plants. The presence of the woody species provides habitat-conditions somewhat like those in the oak-hickory forest proper. That conditions are more xeric is shown by the wider spacing of trees, their shorter stature, and the presence of western species on some hilltops and in prairie islands. Opuntia may be found scattered throughout most of the savannah area and Buchloe may become the dominant grass following chronic overgrazing. Along streams in the savannah the woodland is more forest-like. These flood-plain forests extend far westward into the grassland.

Mean annual rainfall in the savannah area varies between 30 and 40 inches and, in the forest, between 40 and 50 inches. Wind velocity in the herb-stratum is considerably less than in the grassland and consequently evaporation of moisture from the soil surface more gradual. This condition is quite probably an important factor limiting distribution of certain species of toads such as *Bufo a. americanus, Bufo woodhousii fowleri,* and *Bufo cognatus.*

Forested areas in Kansas are almost non-existent. Only small local areas have enough trees to be called a forest. Most of the woodland is confined to stream margins throughout the state. Eastern Kansas has the most extensive floodplain forests as well as almost all the remaining woodland. It is along the streams that the American toad has been able to penetrate westward to the greatest distance. The tall grass prairies of eastern Kansas may be occupied to a limited extent by this toad since it is the common toad of the same prairies further north.

Andropogon furcatus Association (*Little, '38*)

The southern end of the tall-grass prairie extends across east central Kansas and includes the north-eastern sixth of Oklahoma (see figure 1). In Oklahoma it merges eastward with the oak-hickory forest and to the south and southwestward is replaced by the savannah which has just been described. Along the western limits of the tall-grass prairie, mid and short grasses replace the tall species in dominance. Isolated areas of tall-grass prairie occur throughout the eastern part of the savannah area as well as in forested regions. The Grand prairie and the eastern portion of the coastal prairie of Texas resemble the northern tall grass prairie in physiognomy but differ somewhat floristically.

Little ('38) described the portion of prairie occurring in Muskogee County, Oklahoma as an *Andropogon furcatus*[2] climax. He found big bluestem to be the dominant species of grass with *Andropogon scoparius, Koeleria cristata, Manisuris cylindrica, Panicum virgatum, Paspalum floridanum* and *Sorghastrum nutans* as characteristic, associated species. Short-grass species were not found by Little to extend eastward as far as Muskogee county. Most species characteristic of mixed-grass prairie were not found in the tall-grass prairie of Muskogee county. These include *Bouteloua curtipendula, B. gracilis, B. hirsuta* and *Buchloe dactyloides.* On the other hand, the dominance of *Andropogon furcatus* and the presence of *Koeleria cristata* are not associated with mixed-grass prairie in Oklahoma.

The association described by Little extends north-eastward across Craig county and north-westward across Kay county into Kansas (see figure 1). In Kay and western Osage counties *Andropogon scoparius* is the common dominant or is at least co-dominant with big bluestem. Mid-grasses are common in this region and short-grasses are widely enough distributed to become dominant very quickly when overgrazing occurs.

Annual precipitation in the tall grass region is rather high, ranging from 35 inches along the western margin to 40 inches per year on the eastern. This rainfall is adequate at all seasons, although summer drought is the rule rather than the exception.

Andropogon scoparius—Bouteloua curtipendula—B. hirsuta—Buchloe dacyloides Association

The mixed-grass prairie occupies a broad zone between the 97th and 99th meridians and extends from the Colorado river in Texas northward across Oklahoma and Kansas into Nebraska. The area is about 100 miles wide on the average but is very poorly defined on its eastern and western borders where these shift with climatic cycles. Disturbances following the white man's occupation of the region have served to expand the area eastward.

The mixed-grass prairie is so named because of the constant association of short, mid, and tall grasses throughout most of its extent. Dominance is shared by the first two types and the tall species are limited to lowlands or other favorable situations. The mid-grasses, *Andropogon scoparius, Bouteloua curtipendula, Sporobolus asper, S. heterolepis* and other grasses midway in stature between the tall species such as *Andropogon provincialis* and *Sorghastrum nutans* and short species like *Bouteloua hirsuta, B. gracilis,* and *Buchloe dactyloides* are usually dominant in the eastern portion of the mixed-grass prairie while the short grasses are dominant in the western part. The short grasses may occur as small patches among the taller species or the latter may be reduced to scattered clumps or bunches in an almost solid sod of short grasses. The short species are almost always dominant on hilltops with their extent and dominance on hillsides governed by physiographic and edaphic factors operating in conjunction with precipitation. When the mixed-grass prairie is overgrazed, the taller grasses are reduced in abundance or entirely eliminated from the association and the short grasses become the sole dominants. (Bruner, '26, C. C. Smith, '40).

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[2] *A. provincialis* of some authorities and as used in this paper.

One fact to be kept in mind when considering the prairie-regions of Oklahoma and adjacent states is that they are dissected by innumerable small streams and ravines along which more mesic floras extend out into the grassland. It is in such situations that eastern species extend westward into arid regions. A wealth of rough, hilly, and sandy land which serves to introduce edaphic factors into the picture are also present in prairie regions. These facts render any indication of boundaries at best only arbitrary.

The mixed-grass prairie is rendered very distinct in central Oklahoma where, due to edaphic factors, a region which one would expect to have a tall grass climatic climax is covered with an oak-hickory savannah. The savannah area joins a region on the west which is covered with a much "tighter" soil and which has a vegetation on level uplands and hillsides consisting of varying proportions of short and mid-grasses. Prairie islands, found throughout the savannah, may be of mixed-grass or mid- and tall-grass vegetation, depending upon the soil.

Precipitation throughout the mixed-grass region varies between 25 and 32 inches and evaporation 45 to 55 inches per year. Rainfall occurs mostly in fall and spring and the summers are hot and dry.

The dominant plants of the mixed-grass region vary in importance from east to west and in different edaphic situations. In the eastern half of the area the hilltops and upper slopes are dominated by short grasses and the hillsides and upland valleys by mid grasses but with short grasses quite abundant and becoming dominant following protracted drought or continued overgrazing. Bottomland prairies are dominated by a mixture of tall and mid grasses. In the western half of the mixed-grass area the short grasses dominate on hilltops, hillsides, and level upland, and are codominant in upland valleys. Western bottomlands are dominated by mid grasses but both tall grasses and short grasses are present. Sandy soils along the major streams may be covered with cottonwood parkland (Hefley, '37), ash-elm-cottonwood floodplain forest, bunch-grass sand prairie (C. C. Smith, '40), switch-grass prairie, sagebrush or oak shinnery. These types of vegetation are discussed by Bruner ('31) to whom the reader is referred for further analyses.

The fauna of this prairie has received very little systematic study. Dice ('23) studied the vertebrates near Manhattan, Kansas. The works of Phillips ('36), of C. C. Smith ('40, '40a, '40b), of Blair and Hubbel ('38) and of Blair ('39), are the most extensive. So far as the writers are able to ascertain, no work prior to Bragg ('40) has been done which would indicate which Anura, if any, are restricted to the mixed-grass prairie.

Bouteloua—Buchloe Association

West of the mixed-grass prairie lie the short-grass plains. At present in southern Oklahoma the eastern boundary of this area extends from central Stephens and Jefferson counties northwestward around the western edge of the Wichita Mountains in Kiowa County then northward to Blaine County then northwestward through Harper County into Clark County, Kansas, extending across this state through Jewell County on the north. Westward the short-grass prairie extends into the foothills of the Rockies and southward in Texas nearly to the Pecos River, being gradually replaced by desert short-grass. In addition to extensive sandy areas along major streams in the region, in the western tier of counties in Oklahoma and in the Texas Panhandle, large areas of very sandy soil occur which are covered with shin oak, sagebrush, bunchgrass or mixtures of these types. Extensive dune areas also exist. The Salt Plains and Glass Mountains also serve to break the continuity of the short-grass plains. The sandy regions as a rule have few breeding sites for Amphibia except on the floodplains and, as a consequence, the population of these animals is low in such areas.

The short-grass prairies in Oklahoma are characterized by the dominance of blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), with sand drop-seed (*Sporobolus cryptandrus*) and *Aristida purpurea* or *A. longiseta* abundant following periods of drought or overgrazing. Cacti are common in the plains regions. Taller species of grass are present but are limited to areas receiving runoff water from higher areas. Big and little bluestem (*Andropogon provincialis* and *scoparius*) and Indian grass (*Sorghastrum nutans*) are found in the moister situations. Little bluestem often occupies drier areas if the competition from the short grasses is lacking. Thus it is found as almost the only perennial grass in old fields and on roadside banks.

Sandy soils are usually occupied by sandhill grass (*Andropogon hallii*), sand dropseed, sand lovegrass (*Eragrostis trichodes*), little bluestem, sand reed-grass (*Calamovilfa gigantea*), blowout grass (*Redfieldia flexuosa*), sideoats grama (*Bouteloua curtipendula*), blue grama, sand sage (*Artemisia filifolia*), skunkbush (*Rhus trilobata*), shin oak (Quercus spp.), or Prunus spp. in various combinations, depending on soil texture, depth, slope, and position of community on the slope.

Floodplains in the short-grass region are occupied by vegetation composed of switch grass (*Panicum virgatum*), sandhill bluestem, little bluestem, alkali dropseed (*Sporobolus airoides*), muhly grass (*Muhlenbergia arenicola*), feather bluestem (*Andropogon saccharoides*), saltgrass (*Distichlis stricta*), with savannah areas of cottonwood common.

Extensive areas in western Oklahoma and Texas have stands of mesquite (*Prosopsis chiliensis*). Such areas are often referred to as mesquite flats. These diminish in abundance as one proceeds northward across the short-grass prairies and are unknown in western Kansas. Cattle grazing has favored the spread of mesquite.

Rainfall in the short-grass plains country is comparatively low (15–25 inches per year) and evaporation high (50–80 inches per year). Thornthwaite ('31) classifies the region as belonging to the semiarid, mesothermal, rainfall-deficient-at-all-seasons, climatic province.

GEOGRAPHIC AND ECOLOGICAL DISTRIBUTION OF SPECIES OF BUFO IN OKLAHOMA

Seven species or subspecies of toads of the genus Bufo are certainly known from Oklahoma. These are (1) *Bufo americanus americanus* Holbrook, (2) *Bufo cognatus* Say, (3) *Bufo compactilis* Wiegmann, (4) *Bufo insidior* Girard,

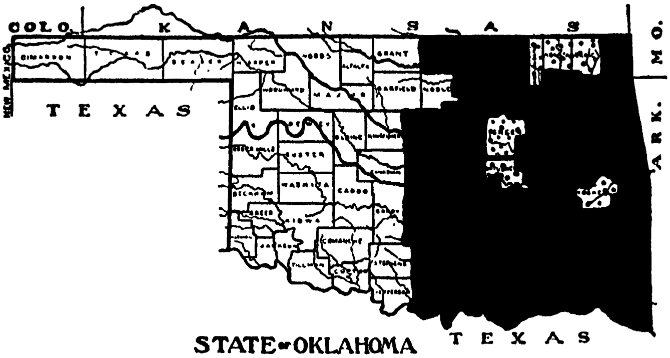

FIG. 2. Known distribution of *Bufo americanus americanus* Holbrook by counties in Oklahoma. The records from Adair and Cherokee counties are from the collection of tadpoles only, that from Ottawa county, by hearing the characteristic call. All others represent specimens examined by us or reported in the literature. Black = known records or specimens: stipple = expected additional range.

(5) *Bufo punctatus* Baird and Girard, (6) *Bufo woodhousii fowleri* (Hinckley), (7) *Bufo woodhousii woodhousii* Girard. *Bufo valliceps* Wiegmann is reported in eastern Texas not far south of the Oklahoma line (most recently by Blair, '41) but so far has not been taken in Oklahoma. Burt and Burt ('29) interpreted with some uncertainty toads taken in southwestern Arkansas near Oklahoma as *Bufo terrestris* Bonnaterre while Black and Dillinger ('38) also indicate that this toad is in Arkansas. Blair ('41), however, restricts the range of this species to the southern coastal plain. If this toad actually occurs in Arkansas, it may enter the southeastern part of Oklahoma, although as yet it has not been discovered in this state.

Definite records of these species in Oklahoma follow in which we give the number of specimens examined by us from each county. It should be remembered, however, that we have actually seen most of these species by the thousands in their breeding congresses and that such specimens are not reported by specific numbers. Records from the literature are given only in cases where we have not seen specimens from the county in question and where we have no reason to doubt the record. The common name used for each species is selected more or less arbitrarily from several which have been used. For others, see Wright and Wright ('33). The scientific nomenclature which we have adopted follows fairly closely that given by Stejneger and Barbour ('39).[3] As Blair ('41) and others have pointed out, the exact taxonomic status of the toads of the *americanus*-group is in confusion but it is hoped that ecological studies will provide a valid basis for taxonomic separation of the species.

Bufo americanus americanus Holbrook (1836) (American Toad)

The American toad is an eastern species ranging from southern Canada west and south to central Oklahoma and east central Texas.[4] It is said to be common throughout its range (Wright and Wright, '33).

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[3] However, we are retaining H. M. Smith's ('34) relegation of *Bufo fowleri* Hinckley to a subspecies of *B. woodhousii* Girard for reasons pointed out on page 305.

[4] Blair's recent paper does not include any part of Texas within the range of this toad. We have found it on the Red River in western Love County, Oklahoma, which gives presumptive evidence of its presence across the river. We have actually seen no specimen from Texas; however, we have heard its call in the northern end of the western cross timbers in Texas.

Its general distribution in Oklahoma is east of a line drawn southward from west central Kay county on the north to western Love county on the Red River (figure 2). The western limit of its range is coincident with that of the oak-hickory savannah in central and southern Oklahoma but it occurs in the true prairie in the northern part of the state and in the broad ecotone between this and the mixed grass prairie in east central Kay county. In the edge of the Oak-hickory savannah from Payne county to the Arbuckle Mountains of Murray and Carter counties, these toads are much dwarfed in size (Bragg, '40b) but from Pattawatomie county southeastward they tend on the average to be larger, although some small ones occur. Where their range coincides with that of *B. w. fowleri* the two are often confused but we have independently observed that the characters given by Blair ('41) will always serve to differentiate them. (See also Myers, '27.) In breeding congresses the two can easily be separated by the great differences in their breeding calls. Since almost all of our specimens have been taken from such congresses, we are confident of our identifications.

Numbers Examined by Counties

Adair, tadpoles; Atoka, 13; Bryan, 1; Carter, 5; Cherokee, tadpoles; Cleveland, 158; Coal, 4; Delaware, 20; Garvin, 4; Hughes, 11; Johnston, 7; Kay, 1; Latimer, 15; LeFlore, 58; Lincoln (Burt, 1935); Logan, 8; Love, 3; Mayes, 1; Marshall, 8; McClain, 1; McCurtain, 35; Murray, 9; Muskogee, 9; Oklahoma, 13; Okmulgee, 3; Osage, 3; Ottawa, call heard; Payne, 7; Pawnee, 2; Pittsburg, 7; Pontotoc, 14; Pottawatomie, 2; Rogers, call heard; Sequoyah, 2; Tulsa, 12. Total examined, 436 adults and many tadpoles.

Bufo cognatus Say (In Long, 1823)
(Great Plains Toad)

The Great Plains toad is present in suitable habitats from southwestern Minnesota (Breckenridge, '38) and Manitoba (Logier, '31) to the eastern foothills of the coast range in southeastern California (Myers, '30). It is also known in northern Mexico. For a map showing general distribution, see Bragg ('40).

In Oklahoma (figure 3) it is generally present west of a north-south line passing through west-central Osage county and slightly west of south through Pottawatomie and Murray counties. In southern Carter county its distribution swings sharply to the westward at the northern edge of the oak-hickory savannah to central Jefferson county then southward to the Red River. It is not known in Love county the southern part of which is largely wooded because of the influence

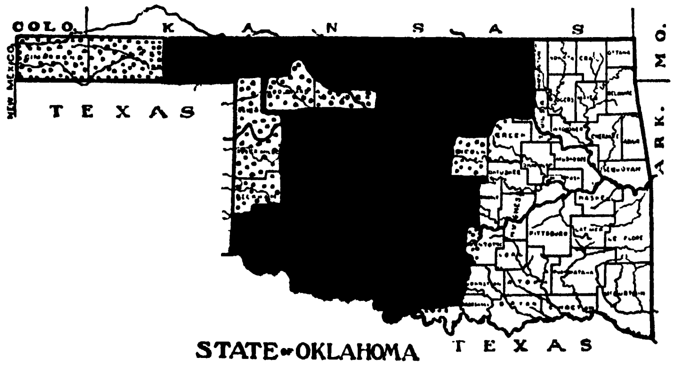

FIG. 3. Known distribution of *Bufo cognatus* Say by counties in Oklahoma. All are from adult specimens examined by us.

of the Red River valley. It will probably eventually be found in the northern part of this county which is largely prairie-land.

Bufo cognatus is the characteristic toad of the mixed-grass prairie and of the larger prairie islands in the western portion of the savannah and it also occurs in the tall-grass prairie in western Osage county, its range extending at least forty miles east of Ponca City. It is also present in the short-grass plains but its numbers thin out rapidly as one passes southwestward through the short-grass area and it becomes restricted to stream banks, irrigation ditches and similar situations. Along the ecotone between mixed-grass and short-grass prairies, *Bufo cognatus* is gradually replaced by *Bufo compactilis* as the characteristic toad. The Great Plains toad has never been taken in the woodland in Oklahoma and it ordinarily does not enter the floodplains of the large rivers (Bragg, '40), although it may do so in very limited areas under special conditions (Bragg, '42b).

Numbers Examined by Counties

Alfalfa, 51; Beaver, 2; Blaine, 22; Caddo, 1; Canadian, 34; Carter, 1; Cleveland, 2398; Comanche, 11; Cotton, 14; Custer, 12; Dewey, 9; Garfield, 27; Garvin, 12; Grady, 6; Grant, 1; Greer, 15; Harmon, 1; Harper, 6; Jackson, 2; Jefferson, 1; Kay, 9; Kingfisher, 19; Kiowa, 2; Logan, 2; McClain, 1; Murray, 11; Noble, 7; Oklahoma, 32; Osage, 32; Payne, 9; Pottawatomie, 2; Stevens, 1; Tillman, 70; Washita, 1. Total examined, 2824.

Bufo compactilis Wiegmann (1833) *(Desert Toad)*

The desert toad is generally distributed from south central Texas through southern Utah and Nevada, southward into Mexico. The northern limits of its range are at present uncertain. It is common in some parts of Texas (Strecker, '15; Wright and Wright, '38) but we have failed to find specific records from the Texas Panhandle. We have one specimen taken in Childress County, Texas, near the Oklahoma line and many specimens from Lubbock county, just south of the panhandle. At Lubbock, Texas, this toad is very common according to information received from Dr. H. M. Hefley to whom we are indebted for the specimens. The junior author spent several nights collecting amphibia in the vicinity of San Angelo, Texas after heavy rains and *Bufo compactilis* was the only representative of the larger Bufos found in that region.

Bufo compactilis was first reported from Oklahoma in 1940 by Bragg and Kuntz and we have since determined it to be very abundant all over southwestern Oklahoma (Bragg, '41b). We have recently found young individuals at the edge of a cattle tank near Buffalo, Oklahoma in Harper county, which extends the known range some 100 miles to the northward and to within about fifteen miles of the Kansas line. This is of especial interest since as late as 1934, no one knew certainly of this toad north of Texas. Our evidence indicates the strong probability that Cope's record for western Kansas, doubted by H. M. Smith ('34), is really valid.

We find *Bufo compactilis* to be strictly limited to the short-grass plains in Oklahoma (figure 4). Its numbers give way very rapidly in the ecotone between the short and mixed-grass prairies as one passes eastward from Washita or Kiowa county and its place is taken by *Bufo cognatus* as explained earlier. On favorable nights, when both species are in large breeding congresses over wide areas, this condition is very apparent. We have transected the ecotone several times and at several places on such nights, always with consistent results.

Numbers Examined by Counties

Comanche, 36; Cotton, 44; Custer, 3; Greer, 48; Harmon, 5; Harper, 2; Jack-

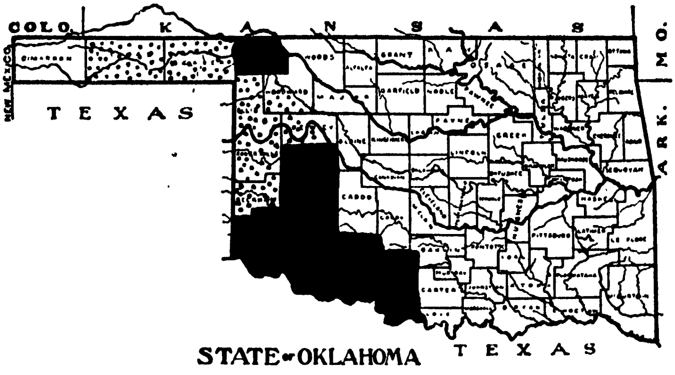

FIG. 4. Known distribution of *Bufo compactilis* Wiegmann by counties in Oklahoma. All are from adult specimens collected and examined by us.

son, 36; Jefferson, 3; Kiowa, 49; Stephens, 12; Tillman, 29; Washita, 3. Total examined, 270.

Bufo insidior Girard (1856) (Northern Little Green Toad) [5]

The northern little green toad is known to range from somewhere in south central Texas north through western Kansas. The exact limits of its range are unknown at present, due in part to its rarity, in part to confusion with *B. debilis*, and in part to its secretive, nocturnal habits. Both H. M. Smith ('34) and Stejneger and Barbour ('39) mention it from New Mexico on the west and the northern part of Mexico on the south. Taylor ('36), who understands the toads of this group probably better than anyone else, knew it from Kansas, Texas, New Mexico, and Mexico (Chihuahua, Durango, and Zacatecas). We have one specimen from Armstrong county in the Texas panhandle for which we are indebted to Mr. Elmo Bonifield who procured it for us.

It has only recently been reported from Oklahoma (Bragg, '41b). We found it breeding in most of the southwestern counties on the night of August 8, 1939 but none were taken on roads. It was congregated at cattle tanks and on the edges of deeper pools in company with *B. compactilis*, *B. w. woodhousii*, *Microhyla olivacea* (Hallowell), *Pseudacris clarkii* Baird, *Scaphiopus couchii* Baird, *Rana sphenocephala* Cope, and sometimes, when the water was clear, with small numbers of *B. cognatus*. The most northern record in Oklahoma is northern Garvin county, but its presence in Kansas makes it very probably present all over western Oklahoma. We are indebted to Mr. Robert Kuntz for a single specimen taken on the streets of Lawton, Comanche county during a summer evening's rain and to Mr. Wayne Randel for another taken at a pool on or near the Murray-Carter county line in the Arbuckle mountains (see figure 5).

Judging from the relatively small numbers found breeding when compared to those of *B. compactilis* on several favorable nights, *B. insidior* is very rare in Oklahoma. For example, on a spring night after a very heavy rain in Greer county, only six specimens of this toad were seen and no others heard even though the whole countryside was one continuous roar with the calls of other species.

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[5] *Bufo debilis* Girard has long been known as the little green toad. Till recently shown by Taylor ('36) to be an error, *B. insidior* Girard was thrown into synonymy with *B. debilis* Girard. Of the three toads in this group now recognized, *B. insidior* is the northern form. Therefore, we propose the common name given above for *B. insidior*, leaving the name, little green toad, for *B. debilis* of southern Texas and Northern Mexico as now understood.

Bufo insidior is primarily a toad of the short grass plains but it enters the mixed-grass prairie for a short distance along its western edge. It therefore shares the range of *B. compactilis* in Oklahoma for the most part but ranges slightly farther to the east and, perhaps, to the west. Neither of them has yet been found in the Oklahoma panhandle, but both are to be expected.

Number Collected by Counties

Comanche, 1; Cotton, 2; Garvin, 1; Greer, 6; Jackson, 8; Kiowa, 3; Tillman, 3; Murray-Carter line, 1. Total examined, 25.

Bufo punctatus Baird and Girard (1852) *(Canyon Toad)*

The general distribution of *Bufo punctatus* was stated by Wright and Wright ('33) to be "south central Texas west to southern California and Lower California." It has since been reported from Kansas (H. M. Smith, '34) and from Arkansas (Black and Dillinger, '38).

In Oklahoma this toad has been formerly reported from three widely separated sections of the state (figure 6). Here, as elsewhere, its distribution seems to be associated with the presence of rocky areas. Jones and Derrick ('39) took juvenile specimens of this toad near a small pool close to White Mound in the Arbuckle Mountains; we collected two specimens in the Wichita Mountains and found hatching eggs in small pools in the rocky ravine below Soldier Lake in the same mountains. There had been several clutches of eggs (probably six or more) produced and all of them were in about the same stage of development. The eggs had been laid in very small pools formed in the solid rock, some of which were no more than one foot square and two inches deep. The eggs were in short files similar to those observed by Strecker ('26), not as described by Wright ('29) as "single or film or scattered mass on the bottom." Dr. A. B. Leonard of the University of Kansas reports to us by letter that he has collected specimens in Woods County, Oklahoma near the Kansas line. New records are included in the county list below. This list actually includes all specimens from Oklahoma of which we are aware. We have never seen the species in breeding congresses, as we have all other species being considered. This is the rarest toad in the state and we know very little about its habits here.

Records by Counties

Blaine, 1; Comanche, 6; Major (Burt, '35); McCurtain (Trowbridge, '37);

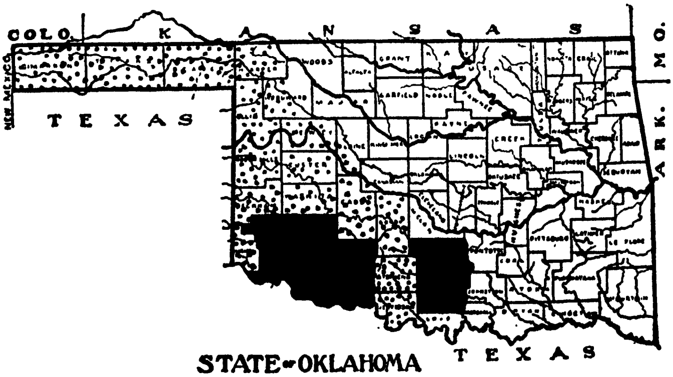

FIG. 5. Known distribution of *Bufo insidior* Girard by counties in Oklahoma. All are from adult specimens collected and examined by us.

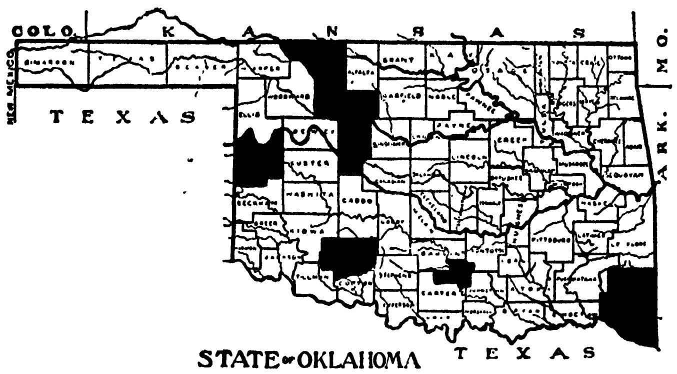

FIG. 6. Known distribution of *Bufo punctatus* Baird and Girard by counties in Oklahoma. Made up from the few specimens seen by us and from the literature cited.

Murray (Jones and Derrick, '39); Roger Mills, 1; Woods (letter from A. B. Leonard). Total examined, 8.

Bufo woodhousii fowleri (*Hinckley*) (*1882*) (*Fowler's Toad*)

Bufo woodhousii fowleri occupies certain ecological situations in eastern and southeastern United States, its exact range being still somewhat uncertain because of confusion with several other species (principally *B. a. americanius, B. w. woodhousii,* and *B. terrestris* Bonneterre) (figure 7). Over the greater part of the East, its geographic range coincides with that of *B. a. americanus* but the range of the latter extends farther north and farther west than that of the former. In Texas the toads of this group are in great confusion, some maintaining that *americanus americanus* does not occur (Blair, '41), others reporting it from several places in eastern Texas. In southern Texas, one group of workers (e.g., Gunter, '41) trace *B. w. fowleri* westward along the gulf to Corpus Christi; others identify the same form as *a. americanus;* but Wright and Wright ('38) call it *B. woodhousii.*

Prior to the initiation of our study, *B. w. fowleri* was known certainly in Oklahoma only in Adair County in the Northeast (Ortenburger, '29a). We have since found it to be the common toad over much of the southeastern part of the state where it is ecologically segre-

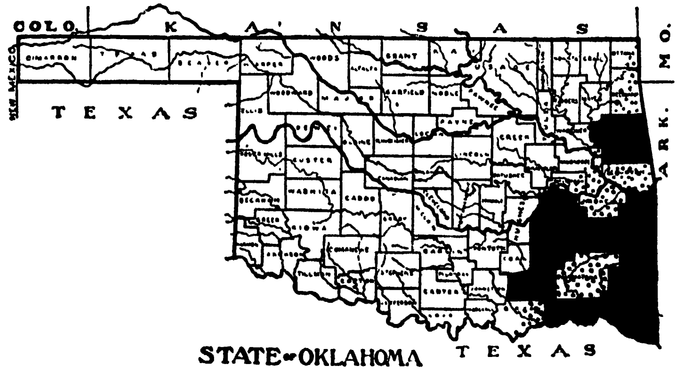

FIG. 7. Known distribution of *Bufo woodhoussi fowleri* (Hinckley) by counties in Oklahoma. Record from Adair county, from Ortenburger ('29a) and from Cherokee county by Blair ('41); the remainder from specimens examined by us.

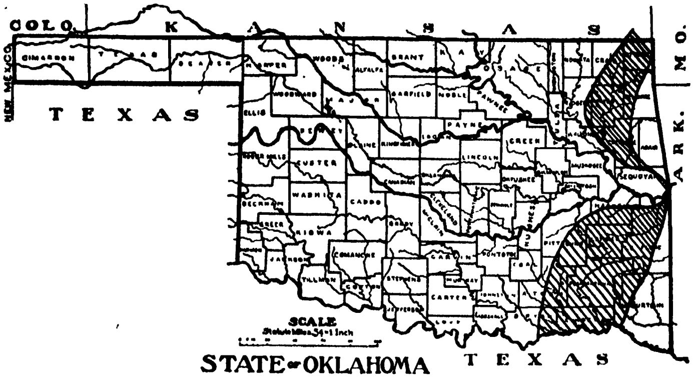

FIG. 8. The approximate limits of the possible intergrading zone of toads of the *americanus*-group in Oklahoma. West of the area designated one may expect to find typical *Bufo woodhousii woodhousii* Girard intermingled with dwarf *Bufo americanus americanus* Holbrook like those described by Bragg ('40b), both widely dispersed in the savannah and the former (but not the latter) extending with *Bufo cognatus* into the grassland. East of the zone, one may expect to find typical members of *Bufo woodhousii fowleri* (Hinckley) intermingling with typical members of *B. americanus americanus* (not dwarfed) and no typical *B. woodhousii woodhousii*. Within the area designated, intergradations of characters occur, especially between *B. w. woodhousii* and *B. a. americanus* in the northeast; less among all three in the southeast.

gated, particularly in breeding, from *B. a. americanus* of the same region. Our observations on this point need no great elaboration for they confirm those of Blair ('41) in almost all particulars.

We have further observed that *B. w. fowleri* is greatly influenced in its breeding activities by temperature, for it breeds only at a higher air temperature than any other toad known to us. On evenings when the temperature is rising, calling begins at about 70° F. and may continue till well after midnight. On the other hand, if the temperature is falling, all calling stops when this temperature is neared or reached. Most calling (as well as actual breeding), therefore, occurs before midnight. These observations, made in southeastern Oklahoma, were clearly confirmed by the junior author at Monroe, La. in the warm spring of 1941 in which region this was the only Bufo which could be found. They also agree in general with some of the first observations ever recorded on the breeding of this toad in Massachusetts (see Cope, '89).

Numbers Examined by Counties

Adair (Ortenburger, '29a); Atoka, 3; Latimer, 6; McCurtain, 20; Pittsburg, 4; Cherokee (Blair, '41); Choctaw, 5; LeFlore, 15. Total examined, 53.

Bufo woodhousii woodhousii Girard (1856) (Rocky Mountain Toad)

The Rocky Mountain toad inhabits the central and southwestern plains and mountains from eastern Kansas, eastern Oklahoma, and east central Texas, westward approximately to the continental divide, although it crosses this in the southwest (figure 8).

If we confine ourselves to typical members of this subspecies in Oklahoma we may say that it is known from nearly every county except in the southeast and the extreme northeast (figure 9). It probably occurs in Haskell county and it may be in western Atoka county, although we have no definite records from these regions. We believe it not to occur from central Pittsburg county southeastward through Pushmataha, southern LeFlore, Latimer, and McCurtain counties; that is, from the northwestern edge of the Ouashita mountains southeastward. *B. w. woodhousii* is the most versatile and the most widely distributed toad in the state. No authentic record from Arkansas was known to Black and Dillinger ('38). We have found it in only one county in Oklahoma on the state boundary, that is, in Sequoyah county. Its eastward extension at this point is probably due to the influence of the Arkansas river, since this toad is partial to sandy floodplains in Oklahoma (Bragg, '40a). From this, one might expect to secure this animal in the region of Fort Smith, Arkansas, as well as in the Oak-hickory savannah in northern LeFlore county, Oklahoma where the oak-hickory pine woodland is interrupted. Although we have no records from this specific area, our expectation, based upon our ecological findings, agrees with the approximate limits of distribution as mapped by Blair ('41).

Numbers Examined by Counties

Alfalfa, 10; Beckham, 2; Beaver, 2; Blaine, 14; Bryan, 4; Caddo, 12; Canadian, 1; Carter, 50; Cherokee, 1; Cleveland, 1077; Cimarron, 14; Coal, 4; Comanche, 106; Cotton, 13; Craig, 1; Creek, 11; Custer, 72; Dewey, 9; Garvin, 37; Grady, 17; Greer, 24; Harmon, 16; Harper, 1; Hughes, 21; Jackson, 3; Jefferson, 7; Johnston, 8; Kay, 20; Kingfisher, 4; Kiowa, 295; Lincoln, 13; Logan, 22; Love, 18; Major, 11; Mayes, 21; Marshall, 8; McClain, 12; McIntosh, 2; Murray, 18; Muskogee, 5; Noble, 1; Okfuskee, 10; Oklahoma, 87; Okmulgee, 13; Osage, 14; Payne, 3; Pawnee, 11; Pittsburgh, 1; Pontotoc, 4; Pottawatomie, 21; Roger Mills (Ortenburger, '26); Rogers, 11; Seminole, 10; Sequoyah, 4; Stevens, 7; Tillman, 24; Texas, 17; Tulsa (Force, '28); Wagoner, 6; Washita, 1; Woods, 47; Woodward, 4. Total examined, 2280.

TABLE I

This table shows the various plant associations through which the various species of Bufo discussed in this paper range. See also figure 11.

	Forest	Savannah	Tall-grass	Mixed-grass	Short-grass	Desert-grass
Bufo woodhousii fowleri	—|—					
Bufo a. americanus	——	——	——			
Bufo w. woodhousii		——	——	——	——	——‡
Bufo cognatus			*†——	——	——	——‡
Bufo insidior				†——	——	——
Bufo compactilis					——	——
Bufo punctatus	restricted to rocky areas in all associations.					

* In prairie islands.
† Enters west edge.
‡ Along irrigation ditches, streams.

Table I presents graphically the distribution of Bufo in Oklahoma as correlated with the major ecological com-

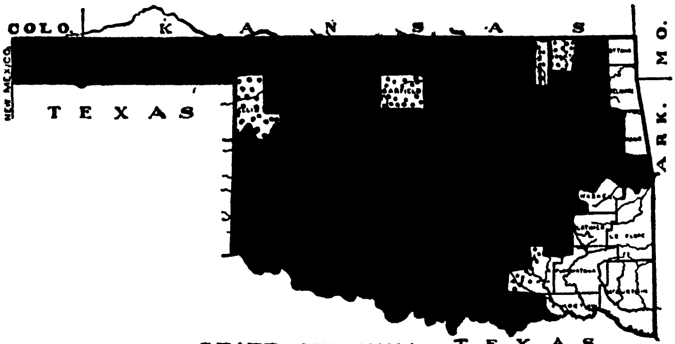

FIG. 9. Known county distribution of *Bufo woodhousii woodhousii* in Oklahoma. Earlier records in the southeast are deleted because based upon specimens of *B. a. americanus* or *B. w. fowleri.*

TABLE II. *Summary of habits of several species of toads*

Species	Feeding Habits	Breeding Habits	Authorities
Bufo a. americanus (American Toad)	Feeds at night during spring and summer when ground is moist. Usually nocturnal and uncommon about streetlights in Oklahoma.	In shallow pools, stream borders, cattle tanks, ditches. During April–June, perhaps earlier; males call from bank, females come into pools during night. Breeding not dependent on rain.	*General:* Miller, '09; Wright, '14; Wright and Wright, '33. *Oklahoma:* Bragg, '40b; Smith and Bragg, '42.
Bufo w. woodhousii (Rocky Mountain Toad)	Nocturnal throughout warm months, often diurnal, especially when young. Common under streetlights even in hot dry weather. Chief habitat, floodplains and bottomlands (sandy soil).	Usually in small groups in either temporary or permanent water. Uses all types of sites except buffalo wallows. Seems to prefer muddy water. Not all mature individuals breed each year. Breeding not dependent upon rain though most frequent after it.	Ruthven, '07; Burt, '32; Pack, '22; Storer, '25; Bragg, '40a, '41; Smith and Bragg, '42.
Bufo cognatus (Great Plains Toad)	Feeds during spring and summer during moist periods, nocturnal but may be active during daytime following rain. Often almost social in feeding activities. Feeds heavily during favorable periods then aestivates in hot dry weather. Uncommon under streetlights.	Huge congresses form after heavy rain in spring or summer (Mar.–Sept.) Uses only temporary, clear water. Flooded fields and buffalo wallows favorite sites. Seldom in tanks, ditches or permanent ponds. Tadpole period between 28 and 45 days (observed), depending on temperature.	Strecker, '10; Bragg, '36; '37, '37a, '40, '40b; Smith and Bragg, '42.
Bufo insidior (Northern Little Green Toad)	Not much known, usually has been taken during or just after rain.	In congresses after big rains. Breeds in temporary pools and streams (latter not observed in Oklahoma). Cattle tanks also used.	Strecker, '15; '26.
Bufo compactilis (Desert Toad)	Much like *B. cognatus* except that it is common under streetlights. "Social feeding" has not been observed.	Will breed in tanks, ponds or any body of temporary water whether clear or muddy. Other habits like *B. cognatus.*	Wright and Wright, '33; Bragg, '40c.
Bufo punctatus (Canyon Toad)	Usually nocturnal, among rocks under which it hides during day.	Probably in small groups, usually in pools in rocks, or in canyons, sometimes in edges of streams.	Storer, '25; Strecker, '26.
Bufo w. fowleri (Fowler's Toad)	Similar to *B. a. americanus.*	Small congresses in early evening when temp. exceeds 70° F., in late May to early July; large streams and pond margins, preferred breeding sites.	Wright and Wright, '33.

munities (see also figure 11). Table II summarizes the habits of these same forms so far as now known.

DISCUSSION

The authors are students of that school of biologists who conceive of all organisms as being grouped into fundamental units on the basis of similar toleration and responses to factors of the habitat. This is a part of the concept of the biotic community. A community can extend no further than the critical range of the factors controlling its development. When these factors exceed a certain limit, some species drop out and others enter or replace them and a new community is then recognizable. The size of the community to be delimited depends somewhat upon the worker and the organisms with which he is dealing. A convenient grouping is to include all portions of the habitat dominated by the same organism. Thus, in a given climatic province, we could have one or several communities, depending upon factors other than climate. Related communities, that is, those having some common components but differing in others, are commonly grouped into associations; and associations with a common physiognomy, into formations.

By recognizing diffuse communities (e.g., aquatic habitats and wooded ravines through a prairie; prairie islands in woodland; woodland islands in prairie; rock outcrops; seeps; etc.) we find that two or more communities may be coextensive geographically and that care must be taken to indicate to which community an organism belongs. For example, *Bufo alvarius* is found only in desert regions yet is not a member of the desert community proper since it lives along streams and irrigation ditches and is somewhat frog-like in its habits (Wright and Wright, '33). Similarly, *Bufo punctatus,* is found in many different associations but is always associated with rocky areas where it spends much of its life in the cool, damp environment provided beneath rocks; and it breeds in small pools in the rocks. It does not associate with the characteristic toads of any association.

Ecological Segregation

It has long been our observation that habits of animals in general and of toads in particular tend to differ in different habitats and that sometimes these differences cut across taxonomic lines. Certain types of habits, especially those of feeding, tend to remain fairly stable whereas those dealing with reproduction may change more markedly as barriers are met in the dispersal of species. Those individuals of any species which change to meet the new situation at a barrier continue to spread their range; those which do not change are stopped.

These changes in an organism may be of three kinds: (1) in structure, without essential changes in habits; (2) in habits without essential change in structure; or (3) in both habits and structure in various degrees of each. If the structure changes sufficiently (whether with corresponding changes in habits or not) we designate a new species; if habits change without essential change in structure, we say that we have a wide-ranging, versatile, species. The greatest difficulty, of course, is centered in those species, subspecies or varieties which change slightly in structure without marked changes in habits.

Since variations in ecological conditions (physical or biotic) markedly effect the lives of individual organisms, and through this, of species, it follows that there is a broader line between the usual ecological emphasis upon succession of communities to the climatic or edaphic climax of a given region, on the one hand, and the taxonomic and geographic distributional emphasis of taxonomists and biogeographers on the other. The study of habits of animals, interpreted in the light of both ecology and taxonomy is, thus, an aid—indeed an absolute essential—to a complete understanding by either group of workers of the peculiar problems of either. This becomes especially true (and there more easily seen) in regions where ecological conditions change radically within a short distance and where, at the same time, two essentially different faunas meet. Similarly, while these principles almost certainly have a wide application, semiaquatic forms in a region of diverse environments can be expected to demonstrate them most clearly. This is one reason why the study of the habits of toads and frogs in Oklahoma was undertaken from the ecological viewpoint.

If we now look again at the distribution of Bufo in Oklahoma we see two toads (*B. a. amercanus* and *B. w. fowleri*) in the more heavily forested areas; two (*B. a. americanus* and *B. w. woodhousii*) in the savannah; three (*B. cognatus, B.*

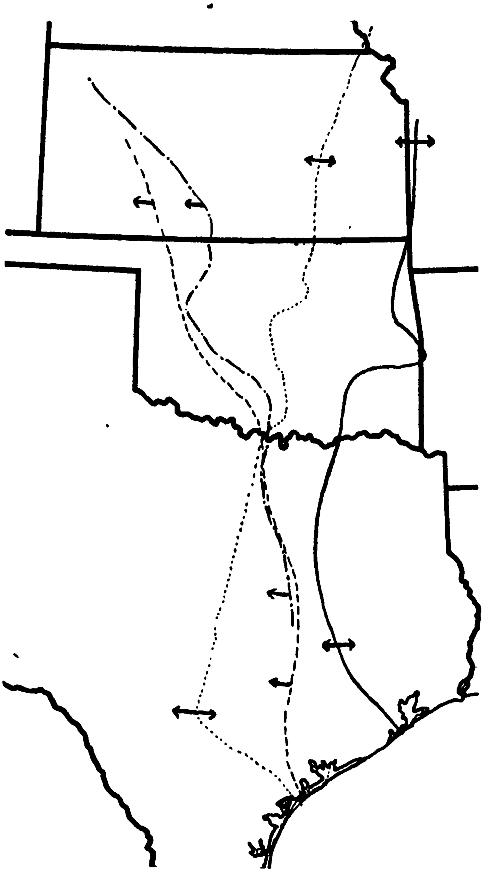

FIG. 10. The approximate east-west limits of the species of Bufo (except *punctatus*) in Oklahoma and adjacent states. Arrows show in what direction each species extends. Solid line, *B. w. woodhousii* to the west, *B. w. fowleri* to the east. Dotted line, *B. cognatus* to the west, *B. a. americanus* to the east. Dashed line, *B. compactilis*. Irregular dashed line, *B. insidior*. Compare with figure 1 to see correlation of distribution with the major ecological associations.

insidior and *B. w. woodhousii*) in the mixed grass prairie; three (*B. a. americanus, B. w. woodhousii,* and *B. cognatus*) in the tall-grass prairie; four (*B. cognatus, B. compactilis, B. insidior, B. w. woodhousii*) in the short-grass plains; and one (*B. punctatus*) which has been taken once in the forest, three times in the savannah, twice in the short-grass plains, and once in the ecotone between the short- and mixed-grass prairies. It is to be noted that some overlapping, both geographic and ecological (figures 10 and 11) occurs among some species but not among others. No species is statewide in its distribution. It is of further interest to observe that each of the species discussed except *B. punctatus* has a part of either the eastern or the western border of its range in Oklahoma. This means that the western group of species (*cognatus, compactilis, w. woodhousii,* and *insidior*) tends to meet the eastern group (*a. americanus* and *w. fowleri*) somewhere within the state and that one could expect the highways for the one group to be the barriers of the other.

The toads of the Oak-hickory forest belong to the eastern group of species, as might be expected from the geographic location of the forested areas. But even there, their ecological distribution differs. *B. a. americanus* is the toad of the mountains whereas *B. w. fowleri* is the toad of the valleys, so that these forms, even though being co-inhabitants of a large geographic area, actually meet ecologically only in local habitat situations somewhat suitable for both. In the extreme southeastern part of the state, *B. w. fowleri* is by far the more abundant, in some localities replacing *B. a. americanus* practically entirely. Farther north, as the land rises rapidly into the pine-covered foothills of the Ouashitas, *B. w. fowleri* and *B. a. americanus* both occur but the former tends more and more to give way to the latter until, as we pass from the Oak-hickory-pine woodland to the Oak-hickory savannah, *B. w. fowleri* disappears completely.

B. a. americanus, however, continues in the savannah, almost immediately becoming associated with *B. w. woodhousii* to the north and particularly to the west. The savannah is progressively drier (in terms of average annual rainfall) as one passes westward but the two toads maintain their numbers well clean to the western edge where this community meets the grassland. But here again, one notes an ecological restriction, though not so marked as between *B. a. americanus* and *B. w. fowleri* in the Oak-hickory-pine woodland. The toads of the sandy flood plains are mostly *B. w. woodhousii,* those of the less heavily wooded hills, *B. a. americanus,* although some of each are to be expected in either situation. In the northern sections of the state, where the Oak-hickory-savannah meets the tall-grass prairie, both of these toads continue into the grassland over the ecotone —although the American toad becomes progressively rarer to the west. Blair ('41) noted that *B. w. woodhousii* was abundant in the Osage prairie and he calls this the prairie toad of the region to distinguish it from the American toad which tends to be confined to islands of the Oak-hickory community here. We have noticed similar tendencies, although we know the American toad to be in the true prairie in the eastern portion.

As pointed out earlier, the ecotone between the Oak-hickory-savannah and the grasslands is very abrupt, due to a sudden change in the fundamental soil type. In the south, this abrupt transition is to short grass plains; in the northeast, to tall grass prairie; and in the larger central portion of the state, to mixed grass prairie. The characteristic toads of the mixed grass prairie (*B. cognatus, B. w. woodhousii*) differ in their behavior at the ecotone. Passing over the ecotone to the west on a night of breeding, one immediately hears numerous calls of *B. cognatus* in the prairie. We have often stood at such times at the edge of the savannah and grassland and noted large choruses of this species on the grassland side, similar but smaller choruses of *B. a. americanus* in the savannah, with calls of *B. w. woodhousii* intermingled with both of the others. *B. cognatus* does not enter the savannah nor *B. a. americanus* the grassland along this transition but the Rocky Mountain toad is here unrestricted.

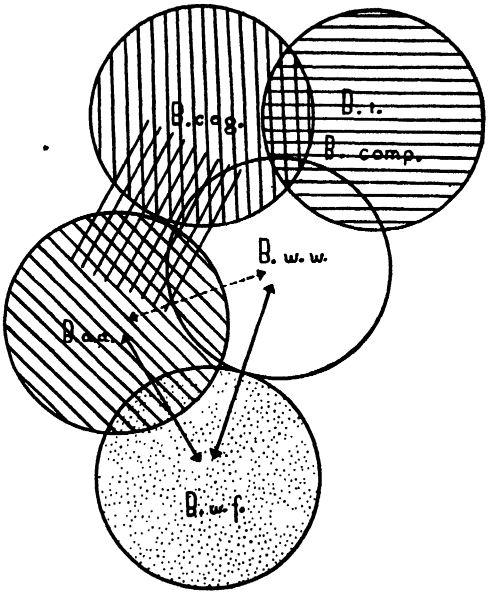

FIG. 11. Diagram showing ecological distribution of Bufo in Oklahoma, *B. punctatus* excepted. Circles represent species (names abbreviated); crosshatching and stippling, ecological association. |||| mixed grass prairie; //// tall grass prairie; \\\\ oak hickory savannah; | | | | short grass prairie; stipple, oak hickory woodland. Arrows indicate probable ability to interbreed in nature (dashed) or known ability (solid). Not shown is the possible hybridization of *B. cognatus* and *B. w. woodhousii* where not sexually isolated (Bragg, 1939).

In the typical mixed grass prairie, however, *B. cognatus* and *B. w. woodhousii* tend to be partially segregated ecologically. The former is more abundant in the higher areas, the latter in the lowlands along the ravines and floodplains. In fact, only exceptionally and quite rarely does the Great Plains toad enter the sandy flood plains or the large rivers at all (Bragg, '40, '42b). There is, however, just enough mixing of the two species at medium elevations so that their partial segregation is not easily apparent. At the extremes, of course, this is more easily seen and we know several areas where it is rare to find a Rocky Mountain toad, the local population being almost entirely of *B. cognatus,* even though in some cases calls of the former may be heard while standing in the midst of a large population of the latter. Repeated detailed collection of toads feeding along roads traversing both types of areas has confirmed our observations based upon calls in breeding congresses.

In the broad ecotone between the mixed and short grass prairie, *B. compactilis* and *B. insidior* join *B. cognatus* as prairie forms, *B. w. woodhousii* continuing here to occupy the same ecological region as before. *B. insidior* is only a minor component of the fauna anywhere in Oklahoma but southwestward, within the short grass plains, *B. compactilis* replaces *B. cognatus* as the conspicuous and abundant form. Both *B. cognatus* and *B. insidior* occur, however, in all parts of the short grass plains in Oklahoma (as well as in the Texas panhandle). In the northwestern part of the state, *B. compactilis* is rarer than farther south and we have not found it in the Oklahoma Panhandle although we predict its presence there. If this toad is extending its range northward (a distinct possibility, though not proved) then it probably is replacing *B. cognatus* as the characteristic form in the short-grass in the Northwest. It is perhaps worth noting in passing that the distribution (both ecological and geographic) of *B. compactilis* in Oklahoma is strikingly like that of the southern spade-foot toad, *Scaphiopus couchii* Baird.

What factors control these distributions? In the first place, it should be recognized that some of these phenomena are probably merely expressions of geographic extensions in time. That is, some species will eventually occupy a larger area whenever they have had time to extend into suitable adjacent areas, as suggested above for *B. compactilis*. However, most of the phenomena are the results of ecological barriers of one sort or another, samples of which are presented below.

B. a. americanus is usually considered to be a medium sized toad of partly diurnal habits. In central Maine, in the White Mountains of New Hampshire, in southeastern Wisconsin and the East generally it is not at all uncommon to find these animals, especially the females, hopping about gardens and lawns in the daytime (observations of the senior author). At and near the western limits of its range in Oklahoma these animals are never diurnally active, are dwarfed in size, and are difficult to find even at night (except when breeding), even though breeding congresses show that a fairsized population occurs (Bragg, '40b). But in the eastern part of the Oak-hickory savannah and in the forested areas of the southeastern part of the state, they average larger (some small ones also occur) and a few may be diurnally active just as is *B. w. fowleri* in the same region.

This suggests that humidity is one of the chief factors limiting distribution of this species and that temperature is another. It seem probable that a climate and soil which favor development of a mixed-grass prairie serve as an absolute barrier to the dispersal of this species. Indeed, it is probable that the American toad is enabled to live at the western limits of the savannah in Oklahoma only through a change to completely nocturnal habits and through becoming dwarfed. In this connection it should be noted that *B. a. americanus* can and does live in tall grass prairie. Presumably the taller grasses serve the same function as trees in the life of this toad in providing shade, moist and cool crevices in which to rest, etc.

It is more difficult to understand the apparent aversion to trees exhibited by *B. cognatus*, nor is it clear why *B. compactilis* has not crossed the ecotone to the mixed-grass prairie. In general it is easy to believe that a progressively dried environment will somewhere stop the spread of a species of frog or toad (as *B. a. americanus* passing westward) but why a progressively moister one should serve as a barrier within the limits of the prairie climates is not at all clear.

One of the most critical areas in Oklahoma occurs along the zone shown in figure 8. This is the area where the ranges of *B. w. woodhousii* and *B. w. fowleri* meet and where *B. a. americanus* is somewhat intermixed with both. Ecological segregation tends to inhibit extensive interbreeding between the American and Fowler's toads (Blair, '41) but this is not so clearly evident between *B. w. woodhousii* and *B. w. fowleri.* In the southern portion of this zone, a small population of *B. w. woodhousii* meets a large population of *B. w. fowleri* and intermingling of individuals is inevitable. This is because both toads are animals primarily of the lower areas such as stream valleys. Furthermore they are not well isolated sexually. The spring breeding of *B. w. woodhousii* begins before that of *B. w. fowleri* but the proclivity of the former to "stagger" its breeding (Bragg, '40a) makes it usual for some individuals to breed later with *B. w. fowleri.* Blair ('41) and others have noted that some individuals from this region give evidence of hybridization and integration and this is confirmed by our own observations. That more intermediates are not found is easily explained on the reasonable assumption that the smaller population of the Rocky Mountain toad is genetically swamped by the much larger numbers of Fowler's toads along the zone of union of their respective ranges. In other words, the morphological characters which distinguish the less numerous western form are blanked out by those which distinguish the more numerous eastern form, so that, whereas integradation in reality occurs, it is less evident than in many other well known cases. In this connection, it is well to remember that *B. w. woodhousii* and *B. w. fowleri* are practically identical anyhow, except as to size (Smith, '34).

In the northern portion of the zone shown in fiure 8, a peculiar variant of *B. w. woodhousii* occurs, which, except for size, strongly suggests *B. a. americanus* (Bragg, '40a).

We found specimens of Bufo in the Arkansas River Valley of northern Oklahoma which appeared to offer evidence of hybridization between the American toad and the Rocky Mountain toad. At Ponca City, we collected a good number of specimens in August of 1939, all of which varied from our concept of typical *Bufo w. woodhousii* and which appear to represent either a cross of *B. w. woodhousii* and *B. a. americanus* or an ecad of the former. In size they are intermediate between the two species. In spinosity and markings they resemble the American toad. Some individuals have spotted venters like the latter species while others have the spots reduced to a single breast spot, a condition usual in *Bufo w. woodhousii* although somewhat variable in specimens from Oklahoma (Bragg, '40a). These forms have been taken together under street lights in northern Oklahoma. We have noticed similarities and differences in the behavior of typical *Bufo w. woodhousii* and the variant. When approached, typical *B. w. woodhousii* commonly becomes alert, sits up straight, and, if blinded by light, sits quietly. The variant remains in a crouched position until approached closely, when it suddenly starts rapidly hopping away and keeps going until out of danger. They usually refuse to sit quietly even when light is shone into their eyes.

We have not collected the variants while they were breeding so have no record of their calls. We have found typical *Bufo w. woodhousii* calling on the banks of the Arkansas River near Ponca City and at that point collected one of the largest female specimens we have seen, the only larger being one taken in Carter county, Oklahoma, the same summer.

Whether these variants are really hybrids or only ecads can be determined only with further field and laboratory work. We do not consider the specimens to be *Bufo woodhousii fowleri* because of their considerably larger size and because they are quite far out of the known range of *B. w. fowleri.*

It is of some interest to note that the breeding habits of the grassland-limited toads (as well as of members of other genera) differ in characteristic ways from those not so limited. This has been mentioned for several species in earlier papers

(Bragg, '40, '40a, '40c, '41a, '42, '42a; Bragg and Smith, '42) but needs reemphasis. The grassland-limited species have the following tendencies in common: (1) breeding only after rain in temporary water, (2) breeding call very attractive to both sexes, (3) tendency to gather quickly into large congresses at breeding, and (4) lack of a definite breeding season (correlated clearly with the stimulus of rain). It is to be specially noted that these tendencies form a breeding pattern especially adaptive to xeric conditions such as found in the drier types of grassland and deserts.

SUMMARY

Since little had been done in delimiting ecological communities in Oklahoma and almost nothing on ecological distribution of toads of the state, it was found necessary to present the ecological communities in some detail, using the dominant plants in the naming of communities, in order to trace the ecological distribution of the toads.

Two biomes are represented (deciduous forest and grassland) with an extensive savannah, mostly between them, related to each. Edaphic factors give savannah in many places where a climatic climax of grassland is to be expected. The forest is limited to the eastern portion of the state, but has long tongues following the major rivers westward into the grassland. The trees of the savannah are largely oaks and hickories, the grasses varying with conditions of climate, soil, and exposure. Pines are locally abundant in the forests of the southeast and four mountain-masses break up the continuity of communities in places. The grasslands are short-mixed-and tall-grass prairies (the first often called plains). In general the tall-grass prairie is in the northeast, the mixed-grass in the central, and the short-grass in the west. "Islands" of one community are common in another, usually due to local peculiarities of soil. Sand prairies of tall grasses and an extensive oak-shinnery community also occur in the west.

We find seven species or subspecies of Bufo to occur in Oklahoma, none of them statewide. *B. a. americanus* is mostly abundant in the savannah but occurs in the woodland and tall-grass prairie. *B. cognatus* is most abundant in mixed-grass prairie, fairly abundant in the plains, and enters the tall-grass for some distance along the ecotone between the tall- and mixed-grass areas. It is never in woodland nor savannah except in extensive islands of prairie and is very rare on floodplains. *B. compactilis* is limited to the plains, in the southern portions of which it is very abundant. *B. insidior* is not numerous in Oklahoma. It occupies the plains, principally, but is present in the western edge of the mixed-grass prairie as well. *B. punctatus* is not an integral part of any of these ecological communities but has been found in several of them in rocky areas only. *B. w. fowleri* is the toad of the lower areas in the woodland only. *B. w. woodhousii* occupies this same nitch in all other parts of the state. In addition, it spreads onto the prairies in smaller numbers.

A zone of varying width occurs along the west edge of the oak-hickory forest in which the population of *Bufo w. woodhousii* from the savannah to the west meets the population of *B. w. fowleri* from the forest to the east. Because of their close relationship and great similarity, hybrids between the two subspecies are difficult to assign to either group. The final assignment usually depends upon which of the group is more familiar to the individual worker. Although the breeding season of *B. w. woodhousii* starts much earlier than that of *B. w. fowleri,* it extends through that of the latter; thus, hybridization is enhanced. The chief differences in these subspecies are a difference in body size and a difference in their calls. Intermediate forms are intermediate in both call and size.

The habits of each of the various species are adjusted to the type of habitats afforded by the biotic community in which it occurs. The American toad has a different habitat here than it does in the eastern part of the United States and is much dwarfed in size at the western limit of its range. Here it is largely nocturnal and more secretive in its habits.

Bufo woodhousii fowleri breeds only when the temperature is about 70° F. and in permanent or semipermanent water. These factors tend to restrict the subspecies to the southeastern United States where the spring is warmer and the rainfall heavier than northwestward, such as in central or western Oklahoma and Texas.

All species of Bufo of the grassland take advantage of bodies of water produced by the first rains of the spring or early summer (where temperatures are not too low) to breed and, in one of them at least (*B. cognatus*), this habit has become so fixed that the species will not breed until or unless the rains come even when there is sufficient water in suitable pools. The "breeding season" which is so commonly mentioned as a part of the life cycle of the species of the East and North tends therefore to be superseded in these drier regions by an absolute dependence upon rainfall and its seasonal distribution. Similarly, these same species tend to have more nocturnal habits than their relatives to the east. All retreat to burrows in the earth or other retreats with the coming of excessively hot, dry weather and remain there till conditions become favorable for their activities. In this way they escape desiccation.

Bufo w. woodhousii usually is found in moist, sandy areas, which in Oklahoma commonly occur along river floodplains. It, too, is largely nocturnal, but it does not aestivate like the typical prairie species nor is it dependent upon the stimulus of rainfall to begin its breeding activities; and it does not often form huge breeding congresses characteristic of the species of the prairie. These habits fit the Rocky Mountain toad to more moist situations such as open woodland, floodplains, and bottomlands where it is the most important and usually the only toad. The habits of *Bufo w. fowleri* differ from those of *B. w. woodhousii* in that the former will not breed when the air temperature is much below 70° F. and the water is not quite warm while the latter will breed when the air and water temperature is below 60° F. and will breed in all types of temporary pools as well as in permanent bodies of water.

These distributions and ecological restrictions apparently apply not only to the biotic associations of Oklahoma but also to those of adjacent states.

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VEGETATIVE AND FLORAL GROWTH OF *FOUQUIERIA SPLENDENS*

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Terminal growth and increment studies have been conducted on many woody plants with particular reference to silvicultural applications, but few studies have been made of plants subjected to xeric conditions. The present report deals with phases of the vegetative and floral growth of ocotillo (*Fouquieria splendens* Engelm.) as representative of long-lived desert shrubs on which growth measurements could easily be made.

Several investigators have studied ocotillo. Robinson ('04) and Humphrey ('31, '35) outlined the manner of petiolar spine formation. The anatomy of the woody stem has been described by Scott ('32), and flower development and embryology have been investigated by Johansen ('36).

METHODS

Measurements of terminal branch increment were taken yearly from 1937 to 1942 on 28 randomly selected plants in the field for a detailed observational study of the vegetative and floral growth of ocotillo. The plants selected for study were marked out on an area 200 feet wide by 800 feet long situated on the grounds of the Carnegie Desert Laboratory near Tucson.[1] Individual branches of each plant were marked to permit yearly measurements of terminal increment at the close of each summer growing season. At the initiation of the study in 1937 it was possible to differentiate and measure the terminal growth-segments of the three preceding years. With subsequent yearly measurements, increment data were collected for the period 1934–42 on more than 700 branches. The total length of each branch, as of 1933, was measured to permit calculation of percentage increment per branch and computation of growth curves.

In addition to the yearly measurements of vegetative growth, data were obtained on the number and length of inflorescences per branch during the spring flowering seasons of 1937, 1939, and 1941. The relationship between vegetative increment and floral growth of individual branches was sought by means of regression analysis.

VEGETATIVE DEVELOPMENT

The unique appearance of mature ocotillo plants is due largely to the manner and sequence of branch development. Mature plants are from 8 to 15 feet in height and in gross structure consist of 40 to 75 or more straight, slender branches which fan out near ground level from a short main trunk. The branches have few laterals as most of their lateral buds remain unelongated and produce clusters of 4 to 12 leaves. As young seedlings, the plants develop several initial branches from a very short trunk. Terminal growth occurs yearly on most of the seedling branches so that these initial branches rapidly attain a height of 4 to 6 feet before additional laterals develop from buds at their basal nodes. Successive development of basal lateral branches after attainment of partial maturity by the parent branches tends to produce a fan-shaped cluster of long straight stems of various lengths radiating outward from the short basal trunk. Terminal growth becomes more and more sporadic as the branches approach maturity, and ultimately ceases when the branches attain a length of from 10 to 15 feet.

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[1] Now occupied by the Southwestern Forest and Range Experiment Station. Acknowledgment is made to Dr. Forrest Shreve for permission to use the grounds of the Desert Laboratory for this study.

Relation of Branch Activity to Age

The amount and frequency of terminal branch increment vary with climatic conditions and with the general age of the individual plant or branch. This is brought out in table I and subsequent data to be presented. The percentages of branches producing terminal increment during the period 1934–42 are shown in table I for the 28 plants under observation. Data are arranged according to relative age of plants as indicated by the total number of branches, and are grouped into two size classes for general comparison. Significant differences may be noted in the percentages of active branches for any given plant among the years included in the study. Certain years, such as 1935 and 1941, are characterized by high percentages of activity among most of the plants while the data for 1940 and 1942 show that little or no branch activity occurred.

Comparison of the percentages for large and small plants within a given year brings out several interesting relationships. Years such as 1935 and 1941, in which a high degree of branch activity is noted, are apparently favorable to both

TABLE I. *Percentages of active branches per plant during the period 1934–1942*

Plant no.	Number of branches	Year								
		1942	1941	1940	1939	1938	1937	1936	1935	1934
Plants with 25 or less branches										
15	6	16	100	33	83	50	33	83	100	75
3	9	7	100	0	55	44	55	12	100	37
7	14	0	95	57	93	69	69	67	80	80
28	17	6	76	0	23	6	12	18	59	75
22	18	0	90	0	83	89	44	19	87	100
4	19	47	84	37	89	84	53	47	73	87
17	21	5	87	0	0	5	0	5	100	52
27	21	0	48	0	0	0	0	5	52	52
6	22	0	50	0	27	0	4	9	50	23
16	22	0	96	54	91	63	26	95	86	100
10	23	0	62	0	13	15	15	8	83	54
23	23	0	77	0	22	48	35	26	73	67
20	24	0	75	0	29	21	0	25	33	9
11	25	0	36	0	0	0	0	0	80	59
Aver.	18.8	5.8	76.9	12.9	43.4	35.3	24.7	29.9	75.4	62.1
Plants with more than 25 branches										
24	27	24	48	4	15	7	7	56	85	80
1	28	0	46	0	0	0	0	14	96	32
2	28	0	68	0	21	14	25	21	89	52
26	31	0	6	0	0	0	0	3	61	23
9	33	0	39	0	0	0	0	0	91	12
25	33	15	82	10	10	17	10	20	90	90
18	34	0	91	9	50	56	0	9	97	92
19	35	0	31	3	14	3	0	18	97	48
14	38	0	58	0	13	10	0	10	71	19
13	44	0	64	9	11	25	7	7	73	50
12	47	0	70	4	2	4	8	21	66	32
5	50	0	48	2	2	4	0	4	80	25
21	53	0	55	2	9	26	9	32	74	55
8	58	0	41	0	3	2	0	3	65	47
Aver.	38.5	2.8	53.3	3.1	10.7	12.0	4.7	15.6	81.1	46.9
Grand aver.	28.7	4.3	65.1	8.0	27.0	23.6	14.7	22.7	78.2	54.5

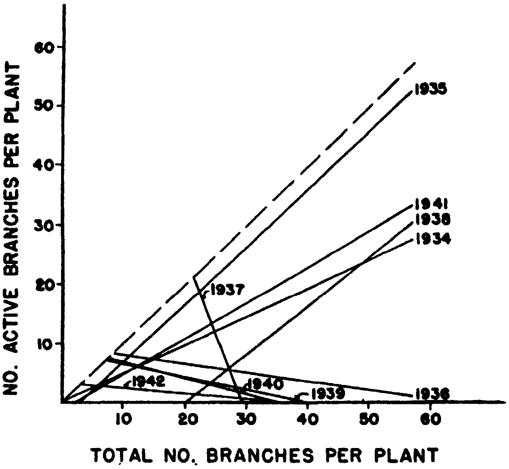

FIG. 1. Regression lines showing relationship of the number of active branches to total number of branches per plant on a yearly basis. Dash line represents 100 per cent active branches.

large and small plants as the older plants had only slightly lower percentages than the younger group. During less favorable years for branch activity, such as the period from 1937 to 1940, greater variability among plants is evident as well as a wider difference between large and small plants. This difference between large and small plants may be seen to better advantage in figure 1 which represents by regression lines the data of table I. They were drawn after plotting the number of active branches against the total number of branches per plant for individual years. During favorable years such as 1934, 1935 and 1941, the numbers of active branches show a positive linear relationship to the total number of branches per plant indicating that a fairly definite proportion of branches produces increment under these conditions. Regression lines for the remaining years, with the exception of that for 1938, indicate a negative relation to exist between the number of active branches and the relative age of the plant as expressed by the total number of branches. These years were unfavorable to branch activity as indicated by the low mean values for percentage of active branches in table I. The general conclusion may be drawn from these data that small or young plants have a high proportion of branches active during both favorable and unfavorable growing seasons and that the larger plants show little branch activity during unfavorable seasons. In favorable years, the number of active branches increases with the size of the plant in a fairly constant ratio.

Further analysis on an individual branch basis of the basic data summarized in table I was made to determine the relationship of branch size to yearly increment activity. In table II, the number of increment intervals added during the 9-year observation period is shown for branches in four height classes. The sporadic increment activity of branches within all height classes is revealed by the small proportion of branches which grew for five or more years, or more than half of the observation period. Of the 732 branches represented in this analysis, not a single branch grew in each of the nine years, although several instances of growth during eight years were noted. The mean values show that 9 per cent of

TABLE II. *Percentages of branches showing 0, 1, 2, etc. increments during the period 1934–1942 according to branch height class*

	Percentage of branches within height class growing									
	0 yr.	1 yr.	2 yrs.	3 yrs.	4 yrs.	5 yrs.	6 yrs.	7 yrs.	8 yrs.	9 yrs.
0.1–1.0 m.	15	8	11	23	20	15	5.5	1.5	1	0
1.1–2.0 m.	5	16	23	24	11	9	6	3.5	2.5	0
2.1–3.0 m.	9	15	33	27	8.5	3	1.5	1	2	0
3.1–4.0 m.	4	22	37	24	9	2	2	0	0	0
Mean	9	14	25	24	12	8	4	2	2	0

TABLE III. *Spring, summer, and total precipitation;* mean increment in cms. of active and total branches per plant; and percentage of active branches during 1934–1942*

Year	Spring rainfall (in.)	Summer rainfall (in.)	Total rainfall (in.)	Mean branch increment per plant	Mean active branch increment	Percentage of active branches
1934	1.85	5.53	7.38	6.24±0.66	11.82±4.8	54.5
1935	7.25	7.09	14.34	12.80±1.03	17.44±7.5	78.2
1936	3.54	5.97	9.51	2.38±0.58	10.84±4.7	22.7
1937	3.52	5.13	8.65	1.29±0.38	10.71±3.2	14.7
1938	2.40	6.42	8.82	2.70±0.52	12.32±5.8	23.6
1939	3.87	3.96	7.83	2.88±0.76	10.64±4.4	27.1
1940	2.12	6.54	8.66	0.90±0.44	10.18±6.0	8.0
1941	7.39	6.31	13.70	10.55±1.07	17.72±8.2	65.1
1942	4.59	3.27	7.86	0.41±0.21	9.06±6.2	4.3

* Precipitation records for 1934 to 1939 inclusive from Carnegie Desert Laboratory; 1940 to 1942 records from University of Arizona. Spring includes December, January, February, and March; summer includes June, July, August, and September; total represents combined spring and summer.

the total branch population added no increment during the same period, although examination of these branches revealed them to be normal in all other respects, producing flowers and foliage comparable to other branches. The highest proportion of these non-growing branches was in the smallest branch height-class. This fact is in agreement with numerous observations of ocotillo plants which show the presence of a number of unelongated, dwarf branches near the bases of the principal laterals. These dwarf branches are probably initiated under extremely favorable conditions and subsequently lose their potentiality for elongation.

Examination of the frequency of increment among the various branch classes reveals that the smaller branches had a higher percentage of increment activity than the older large branches. The highest frequencies noted were in the 2- and 3-year classes. This is in agreement with the basic data of table I which show the years 1935, 1941, and to a lesser extent 1934 to be correlated with a high degree of branch activity.

Relation of Frequency and Amount of Increment to Precipitation

The pronounced variation in branch activity and the definite trends associated with specific years indicated a relationship of vegetative increment to the amount and distribution of precipitation. Comparisons were made of the mean annual increments of active and total branch populations, and of the percentage of active branches with current spring, summer, and combined spring-summer precipitation as shown in table III. Statistical analyses of these data by means of linear regression are presented in table IV.

Seasonal distribution of precipitation in the Tucson area has a marked effect on the vegetative activity of ocotillo plants. The average annual precipitation at Tucson is 11.5 inches, which is distributed in two distinct periods: a winter and spring period from December through March; and a summer period including the latter part of June, July, August, and September. The intervening months between these two periods are characterized by little or no precipitation. In response to these distinct rainy periods, ocotillo plants come into leaf twice during the year; first, with the beginning of the winter-spring rains, and later, at the start of the summer rainy period. Plants retain their foliage as long as the amount and frequency of rainfall is sufficient to maintain available soil moisture. During years characterized by widely-separated storm periods within a rainy season, ocotillo plants may have several periods of folia-

TABLE IV. *Regression coefficients, standard errors of estimate, and t tests for significance of branch increment and percentage activity on spring, summer and total precipitation*

		Percentage of active branches	Mean increment active branches	Mean increment all branches
Spring	Regression coeff.	$8.01X+0.6$	$1.36X+6.76$	$1.60X-2.68$
	St. error of estimate	22.0	1.51	3.22
	t test	Not sign.	Highly sign.	Sign.
Summer	Regression coeff.	$10.87X-27.5$	$1.60X+3.37$	$1.93X-3.37$
	St. error of estimate	24.0	2.56	3.98
	t test	Not sign.	Not sign.	Not sign.
Total	Regression coeff.	$9.72X-60.6$	$1.13X+1.41$	$1.48X-9.86$
	St. error of estimate	18.5	1.24	2.46
	t test	Highly sign.	Highly sign.	Highly sign.

tion and defoliation. Terminal growth occurs principally during the summer rainy period in the vicinity of Tucson, although occasional instances have been noted of spring increment. Inflorescence development is associated with the spring rainy season and continues into the presummer drought period in April.

Table III brings out several relationships of vegetative increment and branch activity to seasonal and total precipitation for the plants under observation. The years 1935 and 1941 were characterized by the maximum percentages of active branches as well as the largest branch increments. These two years were definitely above average in both spring and summer precipitation and, accordingly, in total rainfall. The year 1942, characterized by extremely low summer rainfall combined with a moderate amount of spring precipitation, was the least favorable to ocotillo growth. Minimum values for percentage branch activity and increment for the observation period occurred during this year. Years such as 1938 and 1940, exhibiting fairly high summer rainfall but low amounts of spring rainfall, show only average to minimum increment activity. The data on mean increment of active branches are remarkably uniform and show no significant differences except for the two years of high rainfall, 1935 and 1941. Despite the small yearly variation in active branch increment, the wide fluctuations in percentages of active branches associated with rainfall variation result in a widely fluctuating total increment per plant.

Statistical examination of these data for relationships of increment and branch activity with seasonal and total precipitation was made by linear regression analysis. The method of least squares, using the equation

$$E = \bar{y} + \frac{Sxy}{Sx^2}(X - \bar{x})$$

furnished the regression coefficient presented in table IV. Fisher's tables for the significance of values of *t* were utilized in determining the significance of the relationships.

The regression analysis indicates a positive relationship between amount of precipitation and vegetative increment of ocotillo. Highly significant regression coefficients were obtained between combined spring-summer precipitation and the amount of increment per branch, and between spring-summer precipitation and the percentage of branches producing increment. Comparison of the regression coefficients for spring and summer precipitation indicates that this direct relationship between increment and combined spring-summer precipitation is largely governed by spring rather than summer rainfall. The lack of relationship between current summer precipitation and increment, as indicated by the non-significant regression coefficients, is fairly conclusive from this limited analysis as the individual precipitation values were widely scattered. The highly significant relation found between percentage of branches active and total precipitation is not reflected in either spring or summer rainfall alone, but is apparently due to the cumulative effect of the combined periods.

These relationships of branch increment to precipitation are in substantial agreement with other observations regarding vegetative activity of the plant. In the Tucson area the nearly equal division of rainfall between the spring and summer seasons tends to favor the accumulation of food reserves in many plants during the spring growing season. Cool temperatures and prolonged rains of gentle intensity during the spring create a climate which prolongs the period in which soil moisture is available in contrast to the warmer temperatures and sudden storms with low amounts of infiltration characteristic of the summer rainy season. As a consequence ocotillo plants, which bear foliage only when soil moisture is available, are better able to accumulate food reserves during the spring rainy season than during the summer when soil moisture may be available at more irregular intervals. The cool temperatures of the spring rainy season may further aid in the accumulation of food reserves in contrast to the high summer temperatures which favor rapid respiration.

Interrelationships among Individual Yearly Increments

The variations noted in amount of increment and percentage of branch activity as correlated with age and climatic fluctuation led to a further examination of the increment characteristics of individual branches. To determine whether there was any consistency in growth of specific branches from year to year, the active-branch population of each year was analyzed to determine the proportion of branches which grew in consecutive years and the proportion which grew intermittently. Figure 2 presents graphically this analysis for the period 1934–42; the chronological series of nine graphs represents the continuity of growth throughout the entire observation period of the active-branch population for the years indicated on the left margin. In the graph for each year, the number of active branches of that year is indicated by the broken line. The shaded portion of each bar graph represents the portion of that year's active-branch population which grew in consecutive years from the reference year. Intermittent growth activity of each year's active-branch population is shown by the cross-hatched portions of the bar graphs. In each graph the total number of branches growing during the observation period is represented by the complete bars.

Inspection of the graphs shows the proportion of branches which grew in consecutive years and of branches which grew during intermittent years. For instance, the first graph traces the continuity in growth throughout the observation period of the branches active in 1934. Of the 1934-active population of 379 branches, growth in consecutive years was shown by 307 branches in 1935, 75 in 1936, 15 in 1937, etc., as indicated by the shaded areas in the graphs. The total number of 1934-active branches which grew during the observation period is shown by the shaded and cross-hatched areas, and reference to the broken line shows the proportion of that year's branch population which retains activity. For instance the total number of 1934-active branches which grew in 1936 was 81, 44 in 1937, 83 in 1938, etc. The number of branches growing in consecutive years from the reference year necessarily diminishes or remains constant but the intermittently-active portion of the population, represented by the cross-hatched areas on the graphs, shows a fluctuation dependent upon the total number of active branches.

Differences may be noted in the growth behavior of the active branch populations of favorable years such as 1935 and 1941, and unfavorable growing seasons such as the period 1936–40. Thus 1935 had the largest number of increments of a total population of 763 branches. The proportion of these 1935-active branches which continued growth through the succeeding unfavorable period 1936–1940 was relatively small, except for the year 1936. Of the total branches active during this drought period and in the succeeding favorable year, 1941, more than 80 per

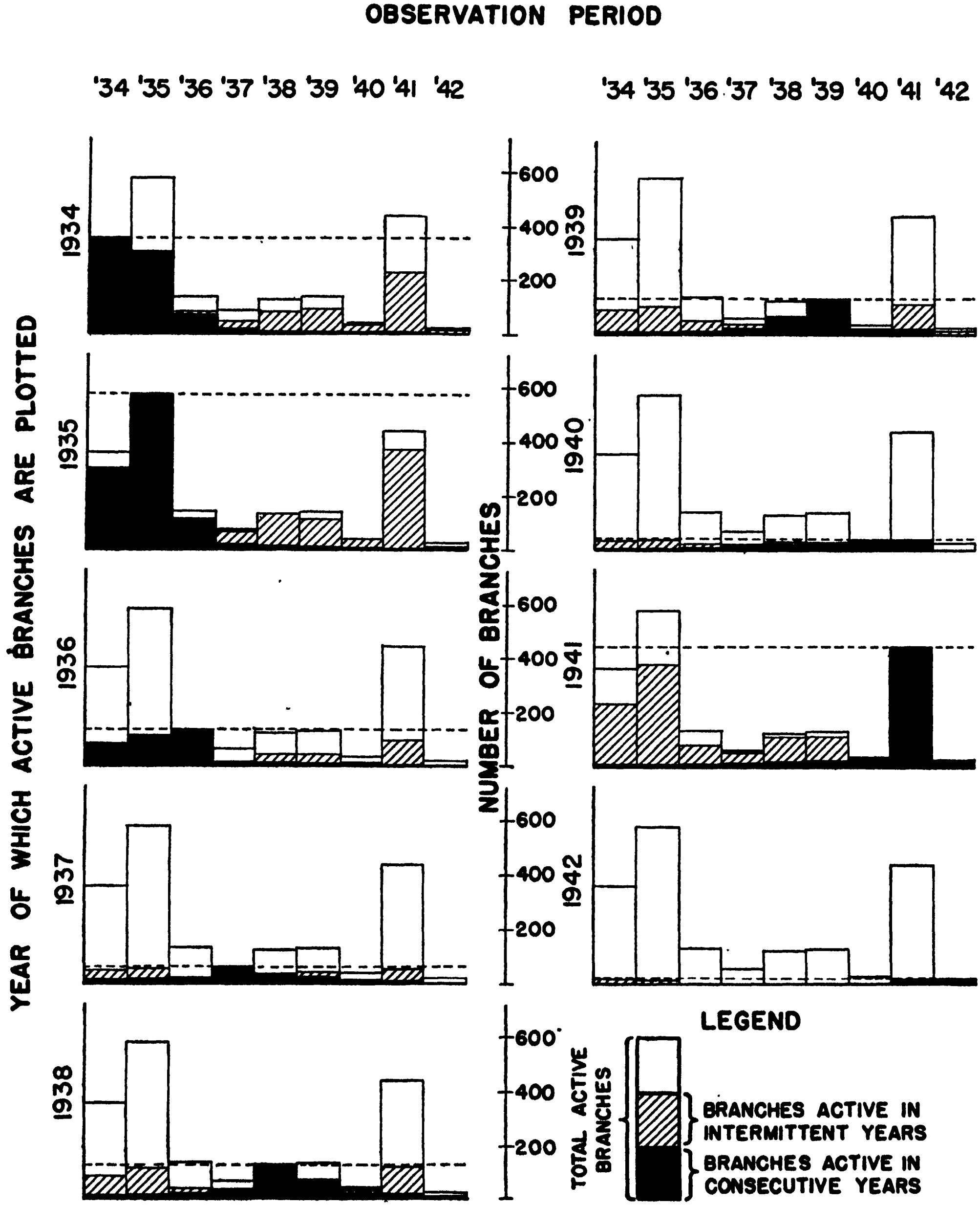

FIG. 2. Continuity in growth of active-branch populations by individual years for the period 1934–42. Broken line represents the number of active branches for the year indicated. Branches growing in consecutive years represented by shaded area; intermittently-growing branches by cross-hatched area; total active branches by complete bars.

cent was made up of branches which had been active during the year 1935. A similar situation exists for the large active-branch population of 1941 and to a limited extent for the 1934 population. The years 1936–1940 showed minimum or small numbers of branches producing increment but the proportion of branches growing in consecutive years during this entire period was definitely higher than noted for the active-branch populations of 1935 and 1941. Comparison of branch growth during favorable and unfavorable seasons thus shows that the branch population producing increment during favorable years includes almost all of the branches active during the poorer years as well as a number of additional branches which grow only under the extremely favorable conditions.

The identity of these branches which grew annually during unfavorable seasons and of those which grew only during favorable years has been indicated in table II. It will be recalled that the smaller branches produced increment at more frequent intervals than the old mature branches as noted in table II and the assumption may be made that most of the branches growing in consecutive years shown in figure 2 are in this small, immature class. Large branches are characterized by sporadic increment as evidenced by the restriction of their terminal growth activity to favorable climatic conditions.

The degree of relationship between the amounts of increment made by individual branches in successive years was sought by a simple correlation analysis. A high correlation between the increments made by the same branches in two successive years would indicate a tendency for uniformity in growth irrespective of the modifying influence of external growing conditions. The low correlation values seen in table V for branches active in both of consecutively-paired years indicate that the amount of increment made during one year has little or no relation to the amount produced during the succeeding year. Low positive and negative correlation coefficients, which were statistically non-significant, were obtained for all but two of the consecutive-year pairs.

TABLE V. *Percentages of active and inactive branches in a total population of 763 branches and correlation coefficients of active-branch increments for consecutive paired years from 1934 to 1942*

	Per cent branches active both years	Per cent branches inactive both years	Correlation coefficient
1934–35	41.5	18.4	+.342 Sign.
1935–36	14.1	20.8	+.136 Not sign.
1936–37	3.5	76.9	+.502 Sign.
1937–38	5.0	76.9	+.099 Not sign.
1938–39	9.7	72.2	+.098 Not sign.
1939–40	4.4	78.8	−.183 Not sign.
1940–41	5.6	41.3	−.165 Not sign.
1941–42	2.4	41.7	−.150 Not sign.
1935–41	50.2	14.6	+.350 Sign.

The significant correlations found in the individual branch increments for the 1934–35 and 1935–41 populations, in comparison to the non-significant relations of the remaining period, point toward a stronger relationship between increments of individual branches during favorable seasons than in unfavorable seasons. The highly-significant coefficient for 1936–1937 increments, years in which a low proportion of branches were active, is the only exception found to this lack of relationship of increments during unfavorable years.

These differences in the effects of favorable and unfavorable years upon the amount of branch activity and increment may lie in the relation of growth to reserve foods in the individual branch. When plants are subjected to a series of low-rainfall years, such as the period 1936–1940, the amount of reserve foods accumulated in a branch during any given year is relatively small. If rainfall is low in amount or infrequent in distribution, ocotillo plants may be partially or entirely defoliated between storm periods and consequently new leaves may develop several times in a single, rainy season. This production of new foliage by the unelongated lateral branch buds maintains the reserve-food accumulations in the branch at a low level so that terminal branch increment is

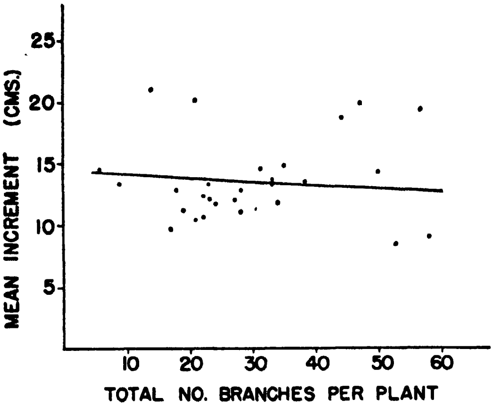

Fig. 3. Relation of mean yearly increment of active branches to total number of branches per plant.

curtailed and only a limited number of branches elongate. When unfavorable conditions for storage of food-reserves continue for several years, as in 1936–1940, branches which grow terminally one season may not grow again for several years until a sufficient food-reserve is developed. As seen in figure 2, the branches which grow in consecutive unfavorable seasons are principally the newly-developing young laterals dependent to some extent upon the parent branch for food reserves. Successive yearly growth of these young laterals and other older branches under conditions of low photosynthetic activity tends toward diminishing amounts of terminal increments. The low positive and negative correlation values between increments made in unfavorable seasons indicate that at least a partial curtailment of increment occurs under these conditions which would tend toward a significantly negative correlation.

When ample soil moisture and nutrients are supplied during rainy periods with evenly distributed precipitation, depleted food reserves may be replenished in a single season in amounts sufficient to enable a majority of branches to elongate. However, the lack of relationship in branch activity noted between a favorable year and a succeeding unfavorable year such as 1935–36 and 1941–42 indicates that availability of soil moisture may become the limiting factor even under conditions of ample food reserves.

Relation of Amount of Increment to Age

Age of plant or branch bears a relation to the amount of increment as well as to the frequency of increment. In figure 3, mean increment of active branches per plant is plotted against the total number of branches per plant as indicative of age. Assuming a direct relationship exists between number of branches and age of plants, a slightly negative relationship is found between mean annual increment of active branches and plant age. Regression analysis of this relationship by the method of least squares yields a regression coefficient of $-.022X + 14.33$ and a standard error of estimate of 3.49 . Application of Fisher's t test reveals that the relationship is not statistically significant as would be indicated by the pronounced scatter of individual increment values.

The scatter diagram reveals a majority of the plants with between 20 and 30 branches to have low mean increment values. No explanation is offered for this fact aside from the vagaries of sampling but attention is called to a similar condition with respect to percentage branch activity in table I for the same group of plants. The low mean increment values of this group of plants account in part for the non-significant relationship of figure 3.

The relation of age of individual branches to mean increment is presented in table VI in the form of yearly increment data by branch-height classes. No significant differences were found in mean active-branch increment with age, although during unfavorable seasons such as the period 1936–1940, the longer branches exhibited the greatest mean increment values. During favorable growing seasons, as for example, 1935 and 1941, there was no appreciable difference in mean increment among branch-height classes. Comparison of increments by years within height classes reveals con-

TABLE VI. *Mean branch increments (cms.) of active branches and percentages of branches active by height classes during the period 1934–1942*

	Year								
	1942	1941	1940	1939	1938	1937	1936	1935	1934
				0.1–1.0 m. branch class					
Increment	7.1 ±5.8	17.4 ±6.5	8.1 ±6.9	9.1 ±3.1	10.8 ±4.5	7.9 ±3.5	8.7 ±5.3	13.6 ±6.3	8.3 ±4.6
Percentage	6	73	5	33	35	20	12	80	57
				1.1–2.0 m. branch class					
Increment	11.1 ±7.1	18.0 ±8.8	7.6 ±4.9	10.4 ±3.9	10.5 ±6.8	8.9 ±3.4	10.4 ±4.5	18.9 ±7.8	12.0 ±4.8
Percentage	6	67	11	19	27	14	17	82	58
				2.1–3.0 m. branch class					
Increment	8.7 ±5.7	17.3 ±8.6	15.5 ±6.0	12.3 ±6.4	12.9 ±3.4	11.4 ±5.8	16.1 ±4.9	20.4 ±8.1	17.0 ±3.0
Percentage	3	61	3	13	11	4	27	74	52
				3.1–4.0 m. branch class					
Increment	—	17.5 ±7.1	—	14.7 ±3.0	17.6 ±13.1	12.5 ±10.6	8.7 ±4.9	19.2 ±7.6	11.0 ±2.6
Percentage	0	63	0	11	8	4	17	89	33

siderable variation between favorable- and unfavorable-season increment, particularly in the smaller branch classes.

Branch activity, as expressed in percentages of branches active in table VI, was greatest among the smaller branch classes during all years except the two favorable ones noted. Thus, in comparison with large or mature branches, the small branches on all plants are characterized by a greater activity in terms of numbers of branches producing increment but conversely by a lesser amount of linear increment per active branch.

The resultant effects of these tendencies for decreased numbers of active branches and uniform or diminishing linear-increment with age of plant are shown in figure 4. Total branch length per plant in 1933 and in 1941 has been plotted against the number of branches per plant as indicative of relative age. The sigmoid growth-curves show that mature plants added the greatest amount of total increment over the 8-year period as evidenced by the greater difference in total branch length in the higher branch-number classes. It is apparent that the decrease in increment with age resulting from a reduction in the number of branches producing increment is more than offset by the increased linear increment per branch, as brought out in table VI.

Further consideration of the growth curves in figure 4 reveals that ocotillo plants increase in number of branches at maturity more rapidly than in total branch length. Mature individual branches tend to reach a definite length and as plants approach maturity, new laterals are produced near the base of the larger branches, and by forking at or near the apices. New lateral branches on all plants are produced only under favorable climatic conditions as evidenced by the fact that 85 per cent of the new branches produced during the 9-year study period developed during the years 1934, 1935, and 1941, which were marked by high percentages of active branches. Many of these new lateral branches on mature plants lose their potentiality for elongation with the result that mature plants often exhibit large numbers of dwarf branches

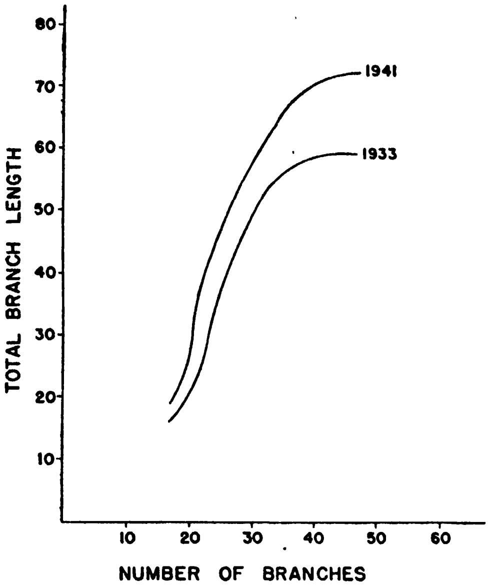

FIG. 4. Relation of total branch length (in meters) to number of branches per plant in 1933 and 1941.

near the point of divergence of mature laterals.

Age of Ocotillo

Plant increment data secured on the study population afforded a unique opportunity to calculate age curves for this species. The sporadic growth habits of individual branches of this species precluded the use of the number of terminal increment segments as a means of establishing age classes of plants, even though individual segments may be distinguished on many mature branches. Casual observation of branch sections revealed a diffuse-porous type of annual ring of insufficient clarity to be readily counted. Frequent occurrence of two distinct terminal increments within the summer growing season, and successive increments in both spring and summer rainy seasons, also invalidated the use of growth rings as an accurate measure of age. Accordingly, terminal increment data for the 8-year period, 1934–41, were utilized in calculating age curves.

Growth curves of branch height and branch number were prepared by establishing a minimum age for small plants and plotting increment additions for 8-year intervals. Twenty-five young plants were measured to obtain total branch length and number of branches per plant. On the assumption that very young plants grow every year, a minimum age per plant was obtained by counting the growth segments on the oldest branch. Mean values obtained for the study area showed that plants with a total branch length of 15 meters had an average age of 23 ± 2.5 years. Using these data as a basis, growth curves were prepared by plotting the increase in branch length with successive 8-year periods as derived from the increment data for approximately 700 branches. Figure 5 presents a growth curve on a branch basis which, together with similar curves prepared on a plant basis, indicates that octillo attains maturity at from 60 to 100 years and reaches a possible maximum age of 150 to 200 years.

INFLORESCENCE DEVELOPMENT

Measurements of the number and length of inflorescences on individual branches were made to determine the relationship of inflorescence development to vegetative increment and climatic fluctuation. Data for three flowering seasons were obtained and the relationship be-

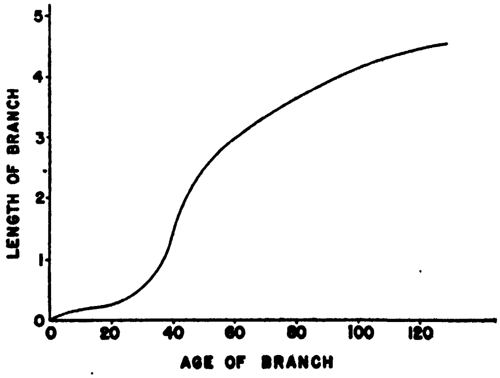

FIG. 5. Relation of branch length (in meters) to age of branch, based on increment of more than 500 branches for the 8-year period, 1934–41.

tween vegetative and floral characters sought by means of regression analysis.

Mature branches were found to produce a greater number of inflorescences than young or immature branches. Figure 6 presents a linear regression analysis of inflorescence number and length plotted against individual branch length as indicative of age. Significant positive relationships were found for data of three seasons which indicate an increase with branch length of the number of inflorescences and the associated variable, total length of inflorescence per branch. Large branches produce several flower clusters at the branch tips and, in some instances, axillary buds of the more recent growth segments may develop inflorescences. Immature branches produce only a few small flower-clusters which are generally terminal. On the samples studied no inflorescences were produced on branches less than one meter in length.

The close similarity in trends of the regression lines for the three seasons gives evidence of the relative independence of floral development of climatic fluctuations. Inflorescence length in 1937 showed a significant difference from that in 1939 and 1941 but the number of inflorescences in the three years was nearly identical. Similar data on vegetative increment (cf. table VI) are characterized by wide variation induced by climatic fluctuation.

Floral development was inversely proportional to the extent of growth of individual branches. Branches of all ages which showed recent terminal increment were characterized by a significantly lower number of inflorescences than inactive branches. Regression analysis of the number of flower clusters per branch plotted against the number of increment intervals added during the 9-year period revealed a negative relationship to exist for the three years in which inflorescence data were obtained. Regression coefficients of this relationship were $-.147X + 1.29$, $-.066X + .909$, and $-.023X + .605$ for the years 1937, 1939, and 1941 respectively. These data are in harmony with those of figure 6 which indicate an increase in the number of inflorescences with age, and with the basic data in table II which ascribe a reduction in increment activity to maturing branches.

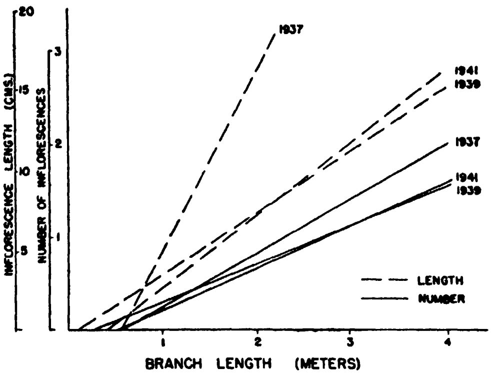

FIG. 6. Regression lines showing relation of the number and length of inflorescences per branch in 1937, 1939, and 1941 to individual branch length.

This tendency for increased floral development with decreased vegetative increment is in agreement with the results of other investigators obtained on annual and perennial plants. Most of the available food reserves in small branches with limited reproductive tendencies is expended in the production of terminal increment and secondary thickening. Increased numbers of inflorescences on mature branches are correlated with the diversion of a large proportion of available food-reserves to the flowers and fruits which results in a checking of vegetative growth. In addition, a portion of the food reserves accumulated by the larger branches may be translocated to the young lateral branches, which results in their tendency for sustained increment and relative independence of climatic variation.

SUMMARY

1. Vegetative increment and inflorescence development studies were conducted on a representative desert shrub, ocotillo, in a field study near Tucson, Arizona.

2. During favorable growing seasons, the number of active branches showed a positive linear relationship to total branch

number per plant; during unfavorable seasons, increment activity was largely restricted to small plants.

3. A positive relationship was found between combined spring-summer precipitation and the amount of increment and percentage of active branches. This relationship was largely attributable to spring rather than summer rainfall.

4. Individual branches of ocotillo tended to increase in amount of increment per active branch but to decrease in frequency of yearly increment intervals with age. The resultant effects of these trends on a plant basis was a greater addition of total increment on mature than on immature plants.

5. Increment studies of the population under observation indicate a mature age of 60 to 100 years for ocotillo plants and a maximum age of 150 to 200 years.

6. Increased floral development was correlated with branch age and with decreased vegetative increment activity of individual branches. Inflorescence development showed greater independence of climatic fluctuation than was shown by vegetative increment.

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A MATHEMATICAL THEORY OF THE GROWTH OF POPULATIONS OF THE FLOUR BEETLE *TRIBOLIUM CONFUSUM* DUV. VI. EGG POPULATIONS IN WHICH THE INITIAL NUMBER OF EGGS IS ABOVE THE LIMITING VALUE

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INTRODUCTION

If a population of the flour beetle *Tribolium confusum* Duv. be set up containing adults and eggs only, and the eggs be prevented from hatching by frequent exchange for new eggs, it will be found that the egg-population increases rapidly at first, but gradually slows down. After a few days or weeks, depending on conditions, it will reach a stable equilibrium and will contain such a number of eggs (ξ) that they are found and eaten as rapidly as laid. This will occur when the eggs number about 32 per gramme of flour. Such populations have been discussed in Stanley ('41 and '42) in which the relation between the volume (or weight) of the flour mass and the number of eggs found at equilibrium, and the relation between the sex-ratio (ratio of females to total number of adults) and this limiting value, were described. It was further shown in Stanley '41 that if the egg population be forced above the limiting value by adding eggs to the population by hand, the egg-number will thereafter decrease to approach the limiting value asymptotically from above. Some data were presented in Stanley ('41) in support of this latter assertion, but it is now proposed to discuss the matter more fully on the basis of better experimental data.

TECHNIQUE

In order to obtain experimental data on the problem, Experiment No. 1 was set up, containing 8 male and 8 female adult beetles in 32 gm. (64 cc.) of sifted whole wheat flour plus 3 per cent of ground wheat germ. The experiment was maintained at 27° ± .05 C., and approximately 75 per cent relative humidity. At the start ($T = T_0$) 8500 eggs were carefully distributed through the flour by prolonged shaking of the flour-egg mixture, and thereafter the egg population was counted every three or four days. The eggs were prevented from hatching by exchange for new-laid eggs at each count. The flour was changed also at the same time. (For further details of technique the reader is referred to Stanley '41, pp. 24–26.) The initial number of 8500 eggs was decided upon as a result of preliminary experiments which showed that this number would be sufficiently large to permit of demonstration of all phases of the prob-

TABLE I. *Decline of an egg-population containing originally 8500 eggs with 8 males and 8 females in 32 gm. (64 cc.) of whole wheat flour plus 3 per cent of ground wheat germ. Maintained at 27° C. and 75 per cent relative humidity. (Experiment No. 1)*

T = time, days	N_2 = no. of eggs at a time, T
0.00	8500
6.10	6454
9.95	5406
11.84	5000
13.86	4563
15.67	4108
18.64	3443
22.60	2869
25.42	2469
29.23	1884
32.55	1516
35.17	1347
38.40	1197
42.35	1080
45.20	998
49.30	965
52.20	907
56.10	916
59.20	920

lem as explained below. The experiment was fortunate in that no beetles died or showed symptoms of illness throughout. The data are shown in table I and are plotted in figure 1 (open circles).

DISCUSSION

Previous theoretical and experimental work (Stanley '41) has shown that there are two phases to be considered in a population containing more than the limiting number of eggs. If the egg-number is above Ω (when the egg-number is equal to Ω the mean-free-path of the adults between successive adult-egg contacts is zero) the eggs are so numerous that they are found and eaten at the maximum rate of which the adults present are capable and the egg-population decreases along a straight line whose slope represents this maximum rate (see Stanley '41, p. 31, Equation (45)). This process continues until the egg population is reduced to the value Ω. Thereafter the rate of decrease lessens, and the egg-population approaches the limiting value ξ asymptotically from above. At ξ the eggs are found and eaten as rapidly as laid. Theoretically ξ is reached only after an infinite time, but in practice it is reached in a few days or weeks, depending upon conditions. We now proceed to discuss the above in greater detail in terms of the mathematical theory developed in Stanley ('41). For the convenience of the reader the notation used in this previous paper is tabulated below, but the reader is advised to consult the previous paper if the following discussion is to be intelligible.

Where

R = sex ratio, i.e. ratio of females to total;
ϵ = number of eggs laid per female per unit time;
N_{11} = number of adults at a time T;
N_2 = number of eggs at a time T;
*$P_{11.2}$ = relative preference of adults for eggs, as food;
$P_{11.1}$ = a similar parameter for flour;
A_2 = percentage of assimilable nutrient material in eggs;
*A_1 = a similar parameter for flour;
*W_2 = weight of an egg;
W_1 = density of uncompressed flour;
$r_{11.2}$ = radius of perception of an adult for an egg;
G = volume of flour used in the culture;
E_{11} = maintenance ration of adults, i.e., the quantity of nutrient material which must be ingested per unit time by each adult to maintain the beetle's normal rate of metabolism, and provide material for normal egg production;
*K_{11} = constant expressive of the compression of the flour due to the forward motion of an adult through it;
*μ_{11} = mean speed of movement of the adult beetles in their random wanderings;
*β = average delay occasioned by an adult-egg contact;

and

$a = R\epsilon N_{11}c - H,$
*$H = E_{11}P_{11.2}\beta\phi N_{11},$
*$\phi = \pi\mu_{11}r_{11.2}^2,$
*$b = R\epsilon N_{11}d,$
$c = A_2W_2P_{11.2}\beta\phi + A_1K_{11}W_2P_{11.1}(\psi - \beta\phi),$
*$\psi = \beta\pi\mu_{11}r_{11.2}^2 - \frac{2}{3}\pi r_{11.2}^3,$
$d = A_1K_{11}W_2P_{11.1}G,$
T = time as measured in days from the start of the experiments,

we have as a general equation descriptive of the course of an adult-egg population in the absence of hatching:

$$T = c_1 + \frac{c}{a}N_2 + \frac{ad - bc}{a^2}\log_e\left[aN_2 + b\right]. \quad (1)$$

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*These symbols are not explicitly referred to in the subsequent discussion, but some of them are implicitly contained in others i.e., $P_{11.1}$ is a part of d, and all are necessary to connect this discussion with previous work, i.e., Stanley ('32, '41, '42).

This is Equation (29)[1] of Stanley ('41) except that the constant of integration $\left(-\frac{ad - bc}{a^2}\log_e b\right)$ has been replaced by its indefinite form, c_1. Later, with a suitable value of c_1, Equation (1) will be used to describe the second phase where $N_2 < \Omega$, $T > T_\Omega$. If, in Equation (1), we set $N_2 = \Omega = \frac{G}{\frac{4}{3}\pi r_{11.2}^3}$, we obtain the equation of the first phase where $N_2 > \Omega$, $T < T_\Omega$, namely,

$$N_2 = \left(R\epsilon N_{11} - \frac{E_{11}N_{11}}{A_2W_2}\right)T + c_2, \quad (2)$$

where the first term in the bracket represents egg additions due to laying, the second term represents egg losses due to consumption of eggs at the maximum rate of which the adults present are capable and c_2 is the constant of integration. Equation (2) is the first integral of Equation (45) of Stanley ('41).

FITTING THE EQUATION OF THE FIRST PHASE

Equation (2) may be fitted to the experimental data of the first phase by choosing suitable values of $N_2 > \Omega$ and

TABLE II. *Computed numbers of eggs for Experiment No. 1 as determined from Equations (3) and (7)*

T = time, days	N_2 = no. of eggs (experimental)	N_2 = no. of eggs (computed)
From Equation (3)		
0.00	8500	8509.67
2.78	7594	7567.42
6.10	6454	6462.02
From Equation (7)		
9.95	5406	5384.22
11.84	5000	5001.62
13.86	4563	4559.51
15.67	4108	4143.67
18.64	3443	3420.92
From simultaneous solution of Equations (3) and (7)		
8.3329	—	5715.9208

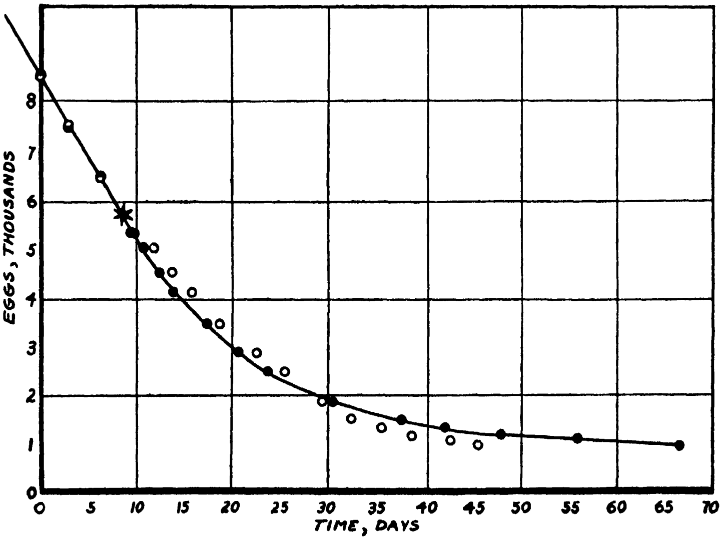

FIG. 1. Experimental and calculated values of T plotted against experimental values of N_2. See equations (3) and (7) and tables II and IV.

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[1] By coincidence this is also a modified form of Equation (29) of Stanley ('32), but the values of a, b, c, d and H given there are now replaced by the improved versions of Stanley ('41).

$T_0 \leqq T < T_\Omega$ and fitting a straight line to them by the Method of Least Squares. Using the points $N_2 = 8500$, $T = 0$; $N_2 = 7594$, $T = 2.78$ and $N_2 = 6454$, $T = 6.10$, we thus obtain an equation:

$$N_2 = 8509.57 - 335.66T. \quad (3)$$

The straight line of Equation (3) is plotted on figure 1 (half solid, half open circles) and the computed values of N_2 for the experimental values of T are shown in table II. It will be noted that the agreement between theory and experiment is quite good.

FITTING THE EQUATION OF THE SECOND PHASE

Equation (1) as its stands, with an indefinite constant of integration, is not well suited to the process of fitting. In order to re-determine the value of c_1, set $T = T_\Omega$ when $N_2 = \Omega$ and

$$c_1 = T_\Omega - \frac{c}{a}\,\Omega - \frac{ad - bc}{a^2} \times \log_e [a\Omega + b] \quad (4)$$

and

$$T = \frac{c}{a}[N_2 - \Omega] + T_\Omega + \frac{ad - bc}{a^2} \log_e \left[\frac{aN_2 + b}{a\Omega + b}\right]. \quad (5)$$

Set $\frac{c}{a} = \delta$, $-\frac{b}{a} = \xi$ (see Stanley ('41), p. 29); then

$$T = \delta(N_2 - \Omega) + T_\Omega\left[\delta\xi - \frac{\xi}{R\epsilon N_{11}}\right] \times \log_e\left[\frac{N_2 - \xi}{\Omega - \xi}\right]. \quad (6)$$

Before Equation (6) can be fitted to the experimental data it is necessary to compute the values of δ, ξ, Ω, T_Ω and $R\epsilon N_{11}$. ξ can be at once determined by averaging the last four values of N_2 from column 2 of table I, giving a mean value, $\xi = 927$. This is admittedly lower than the value $\xi = 1023$ of Stanley ('41) but in view of the rather inexact determination of the value of Ω this difference between the two values of ξ is not serious, and it is proposed to use the value $\xi = 927$ as it stands. The discrepancy may be due to inexact relative humidity control resulting in slight inaccuracies in the flour volume, or it may be due to unavoidable and unknown causes of experimental error.

The values of Ω and T_Ω can be determined by fitting a curve by the Method of Least Squares to a suitable number of points so chosen that one is sure that $N_2 < \Omega$ and $T > T_\Omega$. Using the values

$$\begin{aligned} N_2 &= 5406, & T &= 9.95;\\ N_2 &= 5000, & T &= 11.84;\\ N_2 &= 4563, & T &= 13.86;\\ N_2 &= 4108, & T &= 15.67;\\ N_2 &= 3443, & T &= 18.64 \end{aligned}$$

(see table I), this results in an equation:

$$N_2 = 7126.0969 - 145.7502T - 2.8446T^2. \quad (7)^2$$

The curve of Equation 7 and the straight line of Equation 3 intersect at the point $N_2 = \Omega$, $T = T_\Omega$. Solving these two equations simultaneously we obtain the values $\Omega = 5715.9208$ and $T_\Omega = 8.3329$. These values are tabulated in table II and the point is shown as a six-pointed star in figure 1.

The value of $R\epsilon N_{11}$ may be computed from the original tests for egg-laying rates performed on the 8 females used in Experiment No. 1. The data for these tests are shown in table III. Actually the egg-laying rate was determined for each female each day but nothing is gained in the present case by presenting the data *in extenso*. It is a simple matter to compute the mean value $R\epsilon N_{11} = 66.64$ eggs per day given that $R = .5$ and $N_{11} = 16$.

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[2] An appearance of spurious accuracy is given by the retention of four decimal places in Equation (7). This retention of decimals is desirable, because some stages of calculations in the writer's work show numerous zeros before the significant figures to the right of the decimal point (i.e., calculations leading to Equation (10)–(15) of Stanley '42). As the values in this paper may later be needed for such purposes, the quotation of exact values is worthwhile.

TABLE III. *Data from the preliminary egg-laying tests performed on the 8 females used in Experiment No. 1*

Beetle no.	Total duration of tests, days	Total number of eggs laid	Mean egg laying rate, eggs per day
1	8.96	79	8.81
2	8.97	85	9.47
3	9.03	81	8.97
4	8.95	75	8.38
5	8.74	64	7.32
6	6.77	42	6.20
7	4.80	42	8.75
8	6.80	58	8.52

The values of ξ, Ω, T_Ω, $R\epsilon N_{11}$ and the values of N_2 and T from columns 1 and 2 of table IV are now substituted in Equation (6), resulting in the series of values of δ shown in column 3 of table IV. At first glance the remarkably systematic changes in the values of δ as T increases would seem to indicate that δ did not have a constant value as the theory demands. However, while it may well be true that the theory could be additionally complicated by introducing ageing effects in connection with some or all of the biotic parameters, thus possibly obtaining a non-constant δ, it seems to the writer that the systematic changes in the value of δ as shown in table IV are really more or less accidental. If a mean value, $\delta = +.000{,}055{,}77$ together with the values of the various parameters determined above be substituted in Equation (6), the computed values of T for the various values of N_2, as shown in column 4 of table IV are obtained. When the pairs of values of N_2 and T are plotted as shown by the solid circles in figure 1, it is seen that the theoretical and experimental curves cross each other. It is inevitable then that there should be an orderly trend in the values of δ as determined from the experimental data.

TABLE IV. *Data determined in the fitting of Equation (6) to the experimental data*

T = time, days (exp.)	N_2 = no. of eggs*	δ	T = time, days (computed using mean value $\delta = +.000{,}055{,}77$)
8.3329	5715.9208	——	8.3329
9.9500	5384.22	−.001,552	9.31
11.84	5001.62	−.001,457	10.53
13.86	4559.51	−.001,906	12.10
15.67	4143.67	−.000,928	13.76
18.64	3420.92	−.000,425	17.25
22.60	2869	−.000,464	20.68
25.42	2496	−.000,367	23.62
29.28	1884	+.000,283	30.44
32.55	1516	+.000,803	37.14
35.17	1347	+.001,059	41.82
38.40	1197	+.001,382	47.93
42.35	1080	+.001,776	55.82
45.20	998	+.002,521	66.46

* The first 6 values of N_2 shown in column 2 were obtained from Equations (3) and (7), see table II.

Subject to future correction, the writer is inclined to feel that the discrepancies shown between theory and experiment are due to unavoidable experimental error, rather than to fundamental inadequacy of the theory. That is to say, he feels that the fitted curve is more nearly a true statement of the course of a population of the type under discussion than is the curve traced out by the single experimental example shown. This statement will no doubt lead to raising of eyebrows by some readers, but as the writer's laboratory has had to be closed for the duration of the war owing to military duties, the matter will have to be left in abeyance until more normal times return.

APPROXIMATE COMPUTATIONS OF E_{11} AND $r_{11.2}$

It is possible to extract approximate values of E_{11} and $r_{11.2}$ from the experimental data of Experiment No. 1, as follows: From the data of table III we have that $R\epsilon N_{11} = 66.64$ eggs per day, without regard to sex. During the period $T_0 < T < T_\Omega$ the egg-population decreases according to Equation (3), which is, as stated, the fitted equivalent of Equation (2). Writing Equation (3) in its full form, we have:

$$\begin{aligned} N_2 = {} & 8509.57 \text{ (constant of integration)} \\ & + 66.64T \text{ (eggs laid)} \\ & - 66.64T \text{ (eggs laid and eaten)} \\ & - 335.66T \text{ (original eggs eaten).} \quad (9) \end{aligned}$$

The total consumption of eggs by the N_{11} adults is then $\frac{E_{11}N_{11}}{A_2W_2} = 66.64 + 335.66 = 402.30$ eggs per day. We have from Stanley ('32) that W_2 (weight of an egg) $= .057{,}8$ mgm., and that A_2 (the percentage of absorbable nutrient material in an egg when consumed as food by an adult) $= 55.042$ per cent. We can then readily compute E_{11} as not less than .8 mgm. of dry egg-material per adult per day (disregarding sex differences). As a matter of fact, sex differences do exist, males eating more eggs than females, and moreover, not all the dry material in an egg is absorbable, so that the actual consumption will be more than .8 mgm. per day, and the estimate is very rough in terms of differential consumption by the two sexes. E_{11} could be more accurately computed by allowing adults to feed on dried egg material, and then determining the relative weights of frass and original food. The writer had intended to make this determination, but the war interfered before enough dried egg-material could be collected.

With regard to $r_{11.2}$ it was stated in Stanley ('41, p. 26) that the volume of 32 gm. of the writer's standard flour (sifted whole wheat flour plus 3 per cent of ground wheat germ) is approximately 64 cc. If Ω be considered as approximately 5716, each egg volume (see Stanley, '41, pp. 30, 31) will have a radius of approximately $r_{11.2} = 1.39$ mm. A rough computation based on the physical dimensions of eggs and adults was made in Stanley ('41, p. 36) and gave a value $r_{11.2} = 1.665$ mm. As stated in Stanley ('41), much of the surface of an adult is clearly not perceptive to eggs.

ACKNOWLEDGMENTS

The writer wishes to express his thanks to the Science Research Committee of Queen's University, whose financial support made this research possible. He is also indebted to the National Research Council of Canada for the loan of sundry apparatus. The eggs counts were made by Miss Mary Baker, the writer's Research Assistant, to whom credit must be given for faithful and patient work on this and related problems.

SUMMARY

A population of *Tribolium confusum* Duv. is examined in which eggs and adults only are present, and in which the eggs are so numerous (by reason of artificial additions) that they are above the value at which the adults present can eat them at the maximum rate of consumption of which they are capable. Theory and experiment agree moderately well in showing that in the absence of hatching the egg-number first decreases along a straight line down to this value (Ω) mentioned above, and thence, the egg-number decreases with lessening rapidity to approach the limiting value (ξ) at which eggs are found and eaten as rapidly as laid, approaching ξ asymptotically from above.

Approximate values for E_{11}, the maintenance ration of an adult beetle, and $r_{11.2}$, the radius of perception of and adult for an egg, are computed.

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WATER SUPPLY AND THE GROWTH RATES OF CONIFERS AROUND BOSTON

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The dominance of the water supply factor in determining the relative width of annual ring in New England conifers has been emphasized by the studies reported in recent years. Evidence is accumulating that the rate of secondary growth, aside from the well known changes in width of annual increment due to age of the tree, is limited and to some extent governed by the water available in the soil, much of which is normally supplied during the growing season of the tree. For hemlock and white pine, the correlations between relative growth rates and the precipitation records of certain periods of the year are so high that the occurrence of a notably narrow or wide ring of wood is presumptive evidence for a drouth or a generous supply of water to the tree for the growing season in which it was formed.

Aside from its physiological aspects, this agreement has important bearings on problems of dendrochronology in the area (Lyon, '39 and '39a) and on any future use of the tree ring records of yearly growing conditions for several centuries in the past. Abbot's demonstration ('36) of cycles in the ring widths of certain Vermont hemlocks is a specific example of the uses that can be made of the relationship, provided it holds over a wide area. The use of the cycles in long range forecasting of water supply for plants is an obvious sequel (Lyon, '41).

Since most of the tree ring records compiled thus far in New England have come from Vermont and New Hampshire (Adams, '28 and '35; Lyon, '36 and '40; Goldthwait and Lyon, '37), it will be necessary to compare them with similar records from other states before their use can be extended. There are specific reasons for not expecting close agreement in growing conditions, years by year, for the states north and south of the northern boundary of Massachusetts. The storm centers commonly pass either side of this line which is also close to the junction between forest types. Considerable differences are to be expected between the climatic conditions of inland and coastal New England, with particular reference to rainfall (Brooks, '30; Weber, '28a). On the other hand, Weber ('30) notes that drouths in one section of New England commonly show in other sections to some degree.

One published study of hemlock growth rate in relation to rainfall and temperature (Avery, Creighton and Hock, '40) at New London, Conn., allows a comparison between extremes of north-south and inland-coastal effects. These students of the trees near the Connecticut coast found no significant correlation between growth increment and either temperature or rainfall of certain parts of the year, using all years in the analysis. A check on the years with notably low or high growth rates reveals many discrepancies between northern and extreme-southern New England.

Some unpublished work that can only be touched on here shows that there are also contradictions in this matter of drouth dates in hemlock between western and extreme southwestern New Hampshire, although the trees at the latter site (near Ashuelot, N. H.) cross-dated well with some from central Connecticut. This is evidence for important differences in the dominant climatic factors between northern and southern New England, as they affect the growth of trees. Along the same line, there is a curious difference of one year in many of the dates of maximum and minimum increments of hemlock growth between New Hampshire (Lyon, '36) and northern Pennsylvania

(Meyer, '41). The Pennsylvania trees are usually one year late in recording the pronounced drouths and good years of western New Hampshire.

As an area just southeast of New Hampshire and essentially coastal in its climate, the region of eastern Massachusetts within a short distance from Boston was used for this study. The hurricane of September, 1938, had provided an abundance of fallen pine and hemlock, including the oldest trees of that section. Weather records from several stations nearby are reliable and cover a long span of years. Certain problems there in dating old structures from their timbers require either a long record of measurements of dated tree rings or proof that the ring calendar of Vermont and New Hampshire can be used in the Boston area. The region is also intermediate in latitude between southern Connecticut and northern New Hampshire.

The field expenses for the work were covered by a grant from the Permanent Science Fund of the American Academy of Arts and Sciences which thereby made the study possible. The following persons also aided the project by supplying information about fallen trees or rainfall records: Israel Aubey of Framingham, Dr. C. F. Brooks of Harvard University, L. B. Fletcher of Boston, Dr. Oliver Howe of Cohasset, James R. Simmons of the U. S. Forest Service and J. G. W. Thomas of Lowell.

METHODS AND MATERIALS

The only species of trees sampled in sufficient numbers for use were white pine (*P. strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.), both of which are suitable for tree ring studies for reasons that include the sharp definition of the rings. The other conifers found were too small and scarce for analysis.

Groups of large pine and hemlock still available in 1940 for trunk sectioning were located on various sides of Boston, as shown on the map in figure 1 where the hemlock sites are indicated by solid

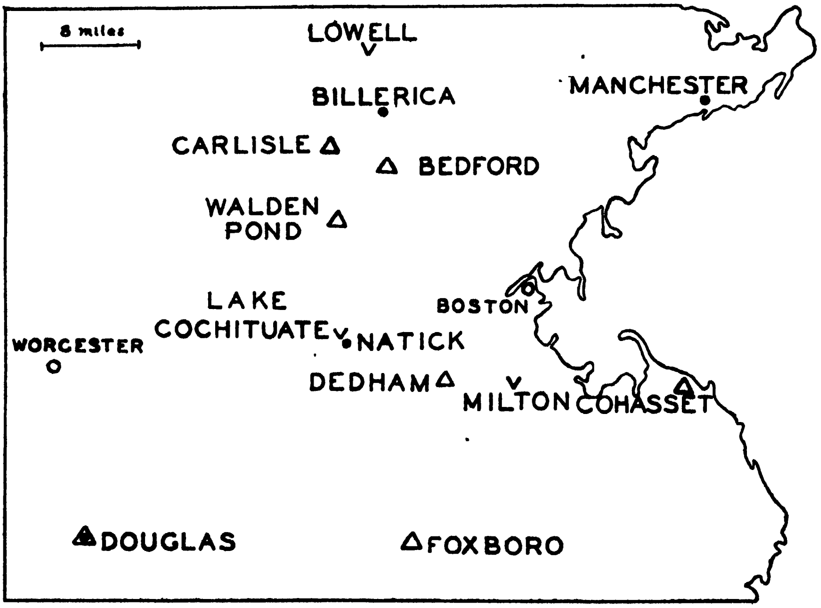

FIG. 1. Map of northeastern Massachusetts showing by solid circles the four sites at which hemlock trees were sectioned; by triangles the seven white pine sites used, and by V's the three weather records stations from which rainfall data were obtained.

TABLE I. *Descriptions of forest sites from which tree sections were taken*

Trees	Locality	Miles to Boston	Slope	Exposure	Soil	Nature of stand
Hemlock	Billerica	19	Gentle	West	Silt	Close, mixed with pine
	Douglas	43	Gentle	West	Stony	Open, with pine and maple
	Manchester	22	Steep	West	Stony	Close, mixed with pine
	Natick	15	Steep	East	Sandy	Open, near base of slope
White Pine	Bedford	15	None	—	Sandy	Open, with small hardwoods
	Carlisle	21	Gentle	West	Stony	Virgin, at foot of slope
	Cohasset	16	Gentle	E & W	Stony	Open, mixed forest
	Dedham	11	None	—	Shallow	Open, among hardwoods
	Douglas	43	Gentle	West	Stony	Open, with hemlock and maple
	Foxboro	24	Gentle	East	Sandy	Close, on low ridge
	Walden Pond	17	Gentle	E & W	Sandy	Open, with small hardwoods

circles and the pine sites by triangles. A brief description of each site is given in table I. Except for sections of both species taken near Douglas, the sites were within 25 miles of Boston, at various distances from the coast. The differences in elevation were negligible in relation to the normal ranges of the species.

The sections were cut transversely at stump height and taken to the laboratory or humid storeroom. They were selected to avoid trunks with irregular rings and trees with growing conditions not typical of the site (Schulman, '41). The principal trees rejected were wide-ringed, complacent pines and all selection was done in the field before the sections were cut.

The measurements were made and recorded according to the technique previously described (Lyon, '36 and '39) and improved by use. The ring widths were read in units of 0.1 mm., with three readings for each ring taken along selected radii. There were no problems of missing or false rings that were not quickly settled by the triple-radius plan. The three measurements for each annual ring of wood corrected errors in the count and identification of rings along any one radius and together provided a reliable index of the increase in diameter of the tree trunk for each year.

Although many of the sections were of trunks over two feet in diameter, the ring counts were surprisingly small. The maximum for pine was 168 (at Carlisle) and for hemlock 144 (at Manchester). In general, the rate of growth was noticeably greater than that of trees in northern New Hampshire. The difference for hemlock was particularly striking and resulted in a comparatively short "calendar" for the region.

The precipitation data for the weather record stations were obtained from official reports brought up-to-date by recent observations. The stations located on the map in figure 1 (Lowell, Milton and Lake Cochituate) provided the rainfall data used in the study of correlations with growth. They were selected for the length and accuracy of their records and for their proximity to sites which gave tree ring records with good "character" for both pine and hemlock trees.

For the purpose of comparing yearly growth rates with precipitation records, the various methods involving correlation coefficients and the like were deliberately avoided in favor of a simpler method of indicating the extent of agreement between the two variables in years giving relatively large or small growth increments. The method is an improved form of that used by Lyon ('36) for hemlock and by Goldthwait and Lyon ('37) for white pine. It relies on the data for the years of maximum and minimum growth rates, the "critical" years in the analysis of relations between growth and water supply because in these years the functional relations are probably less obscured by masking effects of variations in other climatic factors of less importance in the metabolism of the plant. This point is in accord with physiological principles though not accepted by all authors (cf. Glock, '41).

Statistical procedure and data based on trends, departures from an estimated normal, etc., are usually so governed by the measurements in these years of large departures that it is just as accurate to use them alone. In addition to its simplicity of procedure and statement, the method of using critical years for correlation analyses also emphasizes the ecological relations of the years for which there is special interest in the causes, recurrence and possible forecast of unusually good or poor climatic conditions for plant growth. It does not, however, take account of lag and cumulative effects which are generally admitted to influence the effect of precipitation upon the water supply in the soil (cf. Friesner and Friesner, '41).

Growth Records from the Ring Measurements

The measurements of ring width for each trunk section were recorded on forms which included a column each for the average width (mean of three measurements) and the year of growth. The mean ring width for each year was calculated for each group of trees as a unit. These data formed a continuous record of growth rates for the species at any one site.

The number of trees in each group varied from three (one case) to nine, averaging six for hemlock and seven for the pine. The validity of these average measurements, as indices of growth rates for a site, is supported by the good cross-identification from tree to tree within each group and by the use of essentially even-aged stands of forest trees for the sections cut. Whenever there were appreciable differences in the ring counts of the sections, so that the danger arose of a sudden drop in mean ring width for the years when the innermost rings of the younger trees first entered into the calculations, the data for these narrow rings were not used.

The fluctuations in the values of the mean ring widths from year to year are therefore due to environmental factors at the site, chiefly those of climate because the edaphic factors are fairly steady in a forest in relation to the dominant species. The gradual changes in the trend of measurements for each group of trees are due to the well known age factor or to some other non-climatic effect.

The means of the growth increments for hemlock at each of the four sites are shown by separate graphs in figure 2. In the same way but with the vertical scale reduced by 50 per cent, the mean ring widths for the seven groups of white pine are shown in figure 3. For each graph there is a separate base line (marked 0) set just far enough above the next lower one to avoid intersections between any two graphs.

Although these two sets of graphs reveal some interesting points about the forests in which the trees grew, such as the suppression of the Natick hemlocks until about 1870 and the long, slow growth of white pine at Carlisle, they will be used here for what they tell of the abrupt changes in growth rates. For obvious reasons, they are interpreted as revealing changes in climatic factors, possibly those affecting the water supply at the forest site because light and temperature in their direct effects are seldom the limiting factors in such variations of mean growth rates (Pearson, '37).

The principal point of interest in these frequent changes in growth rates, whether they are due to changes in water supply or not, is the extent to which the minimums and maximums in the graphs fall in the same year. If they do, the relatively low or high growth rates are presumably governed by some climatic factor or set of factors varying about the same over an area 40 or 50 miles wide. If they do not agree well in these extremes of

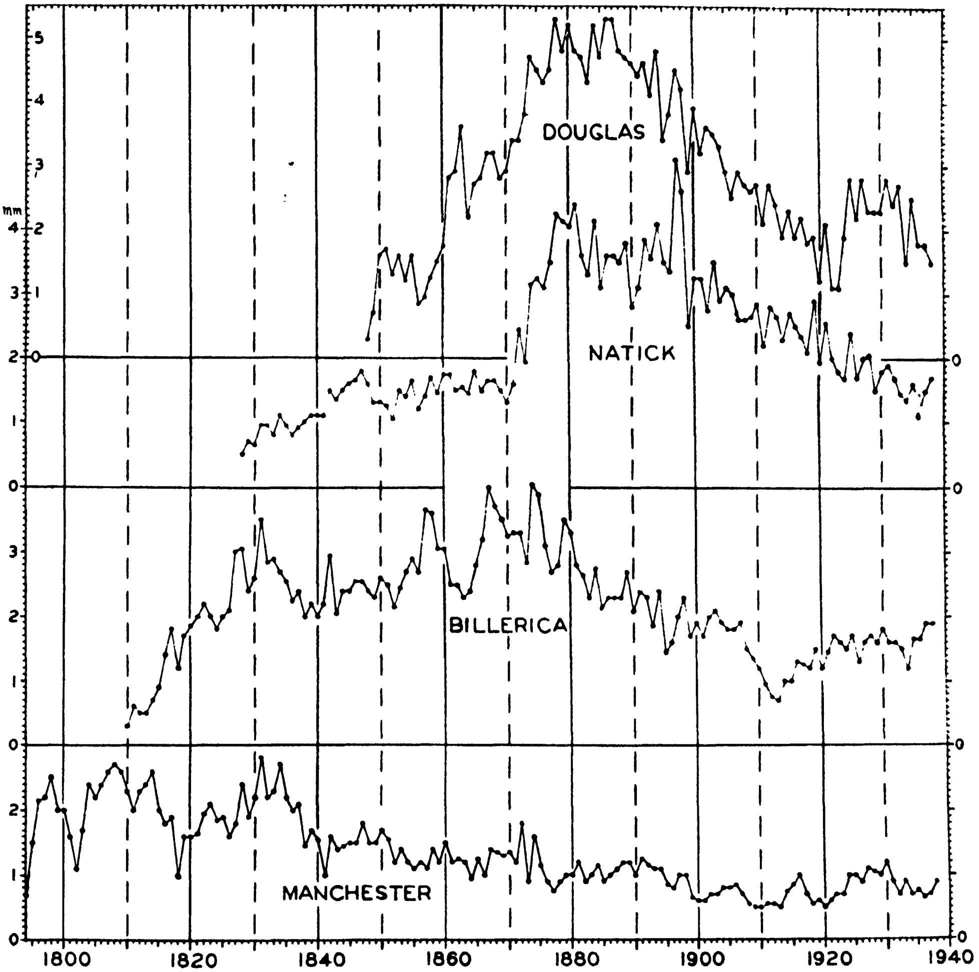

FIG. 2. Radial increments of secondary growth for four groups of hemlock trees at sites named. Mean ring widths on vertical axis read from a separate 0 base line for each graph. The numbers of trees used for the data of each graph were as follows: Manchester, 5 trees; Billerica, 9 trees; Natick, 8 trees; Douglas, 3 trees. For locations of sites, see figure 1. For agreement of crests and troughs, see table II.

fluctuations, the causes for them are probably not widespread. For the other years, the intermediate quantities of a broad, dominant factor would, by pure chance, combine in different years with various combinations of other factors to give unpredictable growth increments, even if all the climatic factors could be described in quantitative terms. Years of agreement in extremes of growth rates are therefore the critical ones for detecting a dominant factor.

From previous work with hemlock and white pine as well as with other species (Lyon, '36, '39 and '40), a perfect agreement of the years for narrow and wide annual rings is not to be expected in this section of the United States. The agreement between sites is highest when the trees are of the same species and the sites are not many miles apart. A distance of 50 miles is not too great for this type of cross-identification under conditions involving no other factors such as coastal

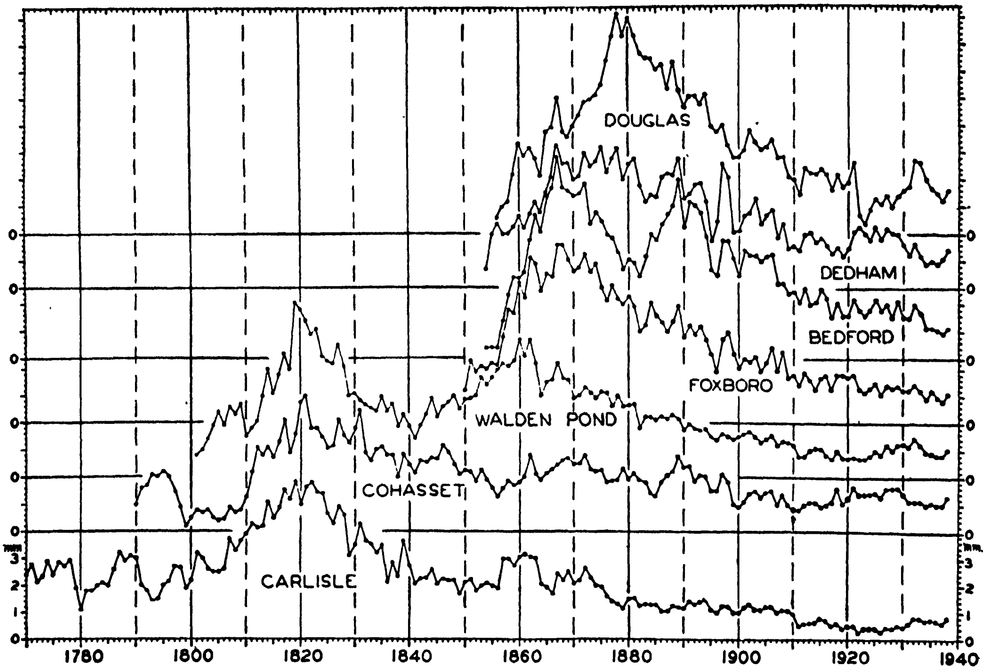

FIG. 3. Radial increments of secondary growth for seven groups of white pine trees at sites named under respective graphs. Mean ring widths on vertical axis read from a separate 0 base line for each graph. The numbers of trees used for the data of the graphs were as follows: Carlisle, 5 trees; Cohasset, 7 trees; Walden Pond, 7 trees; Foxboro, 8 trees; Bedford, 7 trees; Dedham, 7 trees; Douglas, 5 trees. For locations of sites, see figure 1. For agreement of crests and troughs, see table III.

effects or differences in elevation. Within the area being tested, only the Douglas site would seem to be too far away and perhaps too far inland from the others to show nearly the same years of relatively high or low growth rates in a given species.

These years of minimum and maximum growth rates for each of the eleven groups of trees (from ten sites) have been read from figures 2 and 3 and entered in tables II and III to make the comparisons easier. For several reasons, separate tables were used for hemlock and white pine and the corresponding dates common to scattered hemlock sites in New Hampshire were entered in table II for quick comparison.

Because there are often great differences of degree in which a growth rate is shown by the graph of increments to be relatively higher or lower than the rates in years on either side of it, three classes of narrow and wide rings have been indicated in tables II and III (for the data taken from this study). An underscored date means a pronounced minimum or maximum, a date in parentheses is a weak crest or trough on the graph, while an unmarked date is intermediate in this respect. Too much emphasis should not be placed on this classification, however, because it can only be approximate in many cases. Agreement between the sites in this matter of degree of effect of something on growth rate makes the classification correspondingly more significant and often points to certain years as decidedly favorable or unfavorable for the growth of white pine or hemlock or both.

For the purposes of dating sequences of rings in timbers of unknown dates, these tables of critical years form the master "calendars." One for each species is clearly needed here if the unknown wood has a relatively small number of rings and probably so in any case. Yet in many years the response to climatic factors is alike in hemlock and white pine, as Goldthwait and Lyon ('37) noted for northern New England. Notable instances here are 1817, 1867, 1889 and 1897 for wide rings and 1818, 1826, 1829, 1838, 1852, 1864, 1890, 1895-96, 1899, 1926 and 1934 for narrow rings. Perhaps though these only mark pronounced cli-

TABLE II. *Years with narrow and wide rings in hemlock* (from figure 2)

Minimums					Maximums				
Billerica	Douglas	Manchester	Natick	N.H.	Billerica	Douglas	Manchester	Natick	N.H.
1818		1818			1817		1817		
				1821					
1824					1822		1823		
		1826		1826	1827–28		1828		1828
1829		1829		1829	1831		1831		1831
(1832)		1832–33	(1833)	1832			1834	1834	
(1836)		(1836)	1836	1836					
1838		1838							1838
1840		1841		1841	1842		1842	1842	
1843		(1843)	1843						1845
1849				1849			1847	1847	
					1850	1851	1850		1851
1852	1852	1852	1852			1853	(1853)	(1853)	
	1854	1855	(1854)	1854	1855	1855		1855	
(1856)	1856		1856		1857–58		1858	1858	1858
		1859	(1859)	1859			1860	1860–61	
				1862		1863			
1863–64	1864	1864	1864				1865	1865	
		1866	1866		1867	1867–68	1867	1867–68	1867
(1870)	1869–70	(1871)	1870	1869			1872	1872	
1873		1873	1873	1873	1874	1874	1874		1874
1877	1876	1877	(1876)	1877	1879	1878		1878	
			(1880)			1880	1881	1881	1880
1883	1883	1882	1883		1884	1884	1884	1884	
1885	1885	1885	1885	1885		1886–87			
1890		1890	1890		1889		1888–89	1889	
1893	1893		1893		1891	(1892)	1891	1892	1892
1895	1895	1895–96	1895–96	1895	1894	1894		1894	1894
1899	1899	1899	1899	1899	1898	1897–98	1897–98	1897–98	1898
		1900		1900	(1900)	1900			
1901	1901	1901	1902		1903	1902		1903	1903
	1906					1907	(1906)	1910	
1913	1911		1911	1911		1912		1912	
	1914	(1913)	1914	1914		1915		1915	
	1916				1916	1917	1916		1916
1918	(1918)	(1918)	1918	1918	1919	(1919)	(1919)	1919	
1920	1920	1920	1920	1920		1921		1921	1921
(1924)	1922–23		1923–24	1923	1922				
1926	1926	1926	1926		1925	1925		1925	
(1929)		(1929)	1929		(1928)	1927	(1927)	(1927–28)	1928
	(1932)	1932			1930	1931	1930	1931	
1934	1934	(1934)	1934	1934		1933	1933		
		1936	1936			1935		1935	

TABLE III. *Years with narrow and wide rings in white pine* (from figure 3)

Minimums							Maximums						
Bedford	Carlisle	Cohasset	Dedham	Douglas	Foxboro	Walden Pond	Bedford	Carlisle	Cohasset	Dedham	Douglas	Foxboto	Walden Pond
	1799	1799						1801	(1801)				
	1803–6	1804–6				1806							
	1808	1808				(1808)		1807	1807				1807
						1810							1809
	1815	1815				1815		1814	1814				1814
	1818	1818				1818		1817	1817				1817
	1820							1819					1819
								1822	1821				(1823)
	1826	1825–6				1826		1827	1827				1827
	1829	1829				1829		1831	1831				
	(1834)	1833				1834		1835	1835				1835
	1836					1836		1837					1837
	1838	1838				1838		1839	1839				1839
	1841	1841				1841		1844	(1844)				1844
	1845	(1845)				1845			1846				1848
	1849	1849				1849		1851				1851	
	1852	1852			1852				1853				1853
	1856	1856			1856					1860	1860	1860	1860
	1859	1859	1861	1861	1861	1861	1863		1862	1863	1862	1862	1862
1864		1864	1864	1864	1864	1864	1867	1867		1867	1867	1867	1867
	1866			1869				1869	1869			1868	
(1870)	1870	(1870)	1870		1870	1870	1872	1872	1872	1872		1872	1872
(1873)			(1873)		(1873)				(1875)	1875		(1874)	
		1876	1876		1876	1877				1878	1878	1877	1878
1879	1879	1880	1879	1879	1879	(1879)		1880	1879	1881	1880	1880	1881
1882	(1882)		1883		1882	1882	(1884)	1881	(1881)	(1884)		1884	
(1885)		1885	(1885)	(1885)							(1886)		
	1886–7			1887	1887		1889		1889	1889	1888	1889	
1890	1890	(1890)	1890	1890	1890	1890	1891	(1891)	(1891)			(1891)	(1891)
	(1892)	1892			(1892)				(1893)	1893		1893	
1895		1895	1895					1894	(1894)		1894		
1896	1896	1896		1896	1896	1896	1897	1897	1897	1897	1897		1897
	1899	1899	1899	1899		(1899)	1898	1898		1898		1898	
1900	1900	1900	1900	1900	1900		(1901)	1902	1903	1903	1902	(1903)	(1902)
(1904)	(1904)	1904	1904	1904	1904	1904		1905					
	1907	1907	1907		1907	1907	1906	1906	1906	1906	1906	1906	1906
								(1908)	1908	1908	(1908)	1908	
1911	1911	1911	1911	1911	1911	1911							
						1912	1912			1912	1912	1912	
1913										1913			
1914			(1914)	(1914)	1914		1915	1915		(1915)	(1915)	1916	
1917	1917		(1917)	1917	1917	1917	1918	(1918)	1918	(1918)	1918		1918
1919	1919	1919	1919	1919			1921	(1921)	1921	1921	1921	(1921)	
1920	1922				(1920)					1922			
1923			1924	1923	1923		1925			1925	1925	1925	1925
1926	1926	1926	1926	1926	1926	1926	(1927)			(1927)	(1927)		1927
1928				1928		(1928)	1929						
(1931)			1931			(1931)	1932	1932		1932	1932	1932	1932
	(1934)	1934	1934		1934			1933			1933		
1937	1937		1936	1937	1937								

matic effects, particularly in years with very poor growing conditions, for the differences between the species in certain other years are difficult to understand.

Comparison of Growth Rates and Rainfall Records

The ready, though unreliable source of information about the quantities of water made available to the trees is the record of precipitation for the area. It is generally agreed that water supply is important in the physiology of tree growth but it is practically impossible to establish a quantitative connection between the rainfall data and the water that enters the roots. With some degree of connection through the soil assumed, the method of correlations between relative growth rate and relative amount of precipitation at a nearby station was adopted for the demonstration of water supply in the growing season as dominant in the climatic factors of the Boston area.

Using the rainfall records without corrections for runoff of heavy storms and rain falling on moist soil, or for the interception of light rains by foliage and forest litter (Houk, '29), the data from the three stations were assembled for various periods of the year. These were determined by previous experience (Lyon, '36 and '40) and by preliminary tests of new ones, assuming ground storage and shortage effects as well as direct passage into the tree.

The data from each weather bureau station were organized as shown in part by figure 4. The total precipitation at Lake Cochituate is plotted for three periods possibly important for the growth of hemlock at the Natick site three miles east and for white pine at the Walden Pond site ten miles north. Evidence has been offered previously (Lyon, '40) that the relative growth rates of white pine in western New Hampshire do not vary much over these and greater distances from a weather record station. The map in figure 1 shows that the Lowell and Milton stations are no farther from the sites of trees used with their data in correlation studies of other pairs of ring and rainfall records.

For reasons already stated, comparisons were made between rainfall and growth for the years with relatively large or small growth increments, considering the three periods represented in figure 4 and several others including those in tables IV to VI. Periods giving comparisons evidently governed largely by chance have been disregarded.

Correlations between growth and precipitation were recorded as positive, negative or absent according to the following criteria:

Positive if growth rate appeared as a maximum or minimum and if the precipitation was at a corresponding maximum or minimum or markedly above or below the mean for the period and station.

Negative if the growth rate and total precipitation were diametrically opposed in the matter of maximum and minimum.

Absent (or zero) if the relations were like neither of these two categories.

The resulting correlations for the Natick hemlock are shown in table IV and for the Walden Pond pine in table V. In both cases an asterisk before the word "wide" or "narrow" indicates a pronounced crest or trough in growth rate for that year. If either of these words is enclosed in parentheses, the ring for that year was found to be only slightly wider or narrower than the two rings formed in years immediately before or after.

Three other sets of correlations were derived in the same way as follows:

Billerica hemlock growth rate vs. Lowell precipitation

Bedford white pine growth rate vs. Lowell precipitation

Dedham white pine growth rate vs. Milton precipitation

For lack of space, their year-by-year results cannot be presented here but they

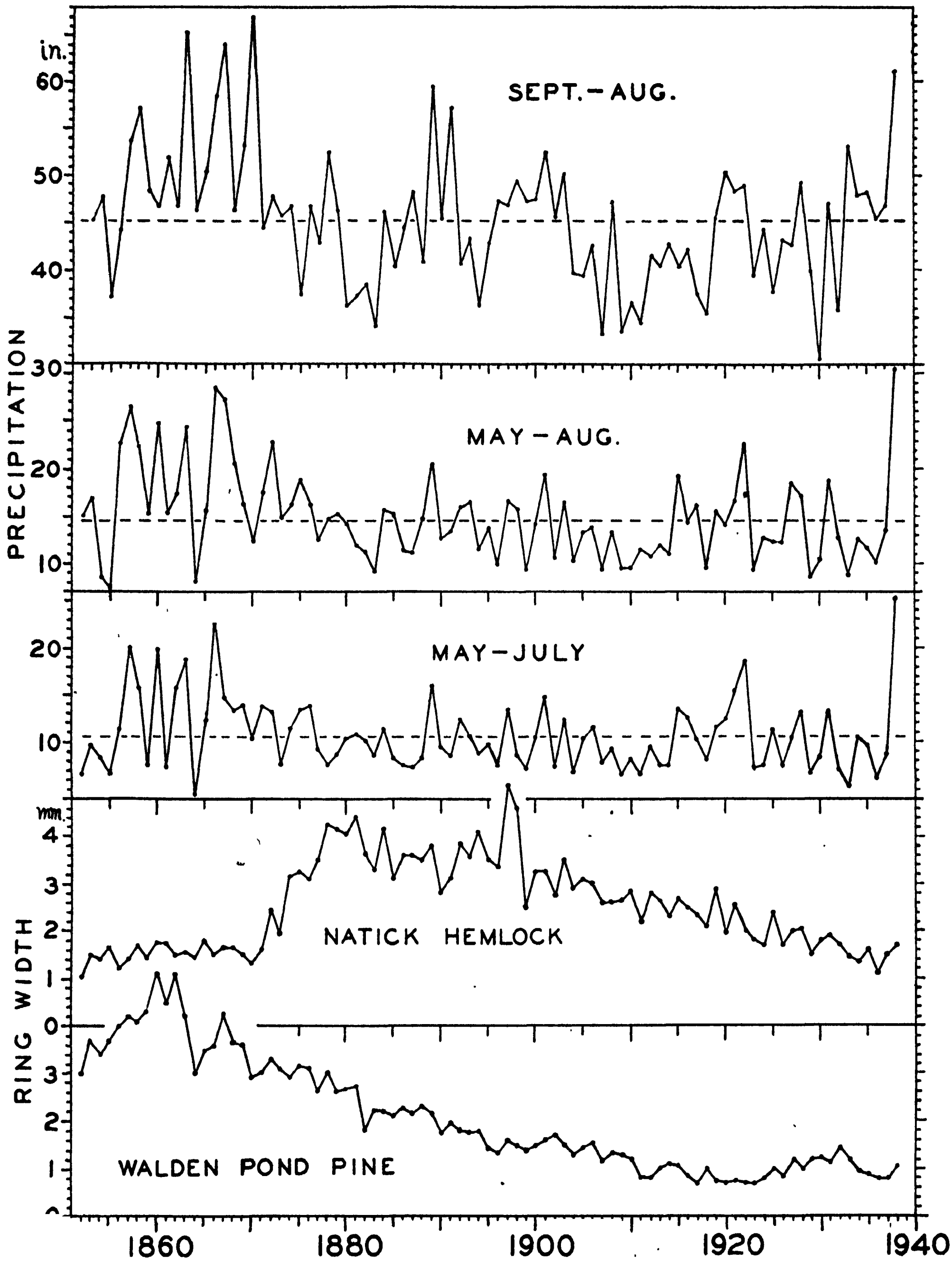

FIG. 4. Mean annual growth increments of eight hemlock trees at Natick and seven white pine trees at Walden Pond (two lower graphs) compared with total rainfall measured at Lake Cochituate station in Natick for certain months as indicated by separate graphs. Broken horizontal lines indicate mean rainfall for the three periods of the year, all months to be read as inclusive. See tables IV and V for correlations between growth rate and rainfall in these and other periods of the year.

TABLE IV. *Natick hemlock growth* vs. *Lake Cochituate rainfall*

+ = positive correlation
0 = no correlation
− = negative correlation

Width of ring	Year	May–July	May–Aug.	Apr.–July	Apr.–Aug.	Mar.–July	Jan.–July	Jan.–Aug.	Preceding Sept.–Aug.	Notes
*Narrow	1856	0	0	0	0	0	+	0	0	
Wide	1858	0	0	0	0	0	0	0	+	Prev. fall wet
(Narrow)	1859	+	+	+	+	+	+	0	0	Prev. fall dry
Wide	1860	+	+	+	+	+	+	0	−	
Wide	1861	−	−	−	+	−	−	−	+	Prev. fall wet
*Narrow	1864	+	+	+	+	+	+	+	+	
*Wide	1865	0	0	0	0	0	+	0	0	
Narrow	1866	−	−	−	−	−	−	0	0	Prev. fall dry
Wide	1867	0	+	0	+	+	0	+	+	Prev. fall wet
Wide	1868	−	0	+	+	−	−	−	−	Prev. fall dry
*Narrow	1870	+	+	−	−	−	−	−	−	
*Wide	1872	+	+	0	+	0	−	+	+	
*Narrow	1873	+	+	+	+	+	+	+	+	
(Narrow)	1876	−	0	−	0	−	−	−	−	Run-off in July
Wide	1878	−	0	+	+	0	+	+	+	
(Narrow)	1880	0	0	0	0	+	+	+	+	
Wide	1881	+	0	0	0	+	+	+	0	
*Narrow	1883	+	+	+	+	+	+	+	+	
*Wide	1884	+	+	+	+	+	+	+	+	
*Narrow	1885	+	0	0	0	+	+	+	+	
*Wide	1889	+	+	+	+	+	+	+	+	
*Narrow	1890	+	+	+	+	0	+	+	+	
Wide	1892	+	+	0	0	0	−	−	−	
Narrow	1893	0	−	−	−	0	−	−	−	Prev. fall dry
*Wide	1894	−	−	−	−	−	−	−	−	Lag from 1893?
*Narrow	1895	0	−	−	−	−	0	−	0	Lag from 1894?
*Narrow	1896	+	+	+	+	+	0	+	−	Prev. fall wet
*Wide	1897	+	+	+	+	+	+	+	0	
*Wide	1898	0	+	+	+	0	+	+	+	Prev. fall dry
*Narrow	1899	+	+	+	+	+	+	+	+	Prev. fall wet
Narrow	1902	+	+	+	+	+	+	+	+	Prev. fall wet
*Wide	1903	+	+	0	+	+	+	+	+	
Wide	1910	+	0	0	−	−	0	−	+	Prev. fall wet
*Narrow	1911	+	−	+	0	0	+	+	+	
Wide	1912	+	−	+	0	+	+	0	+	
*Narrow	1914	+	+	+	0	0	0	0	−	
Wide	1915	+	+	0	+	−	0	+	−	
*Narrow	1918	+	+	+	+	+	+	+	+	
*Wide	1919	0	+	0	0	0	0	0	0	
*Narrow	1920	0	+	0	0	0	−	−	−	
*Wide	1921	0	0	+	+	0	−	−	0	Prev. fall wet
Narrow	1923	+	+	+	+	+	+	0	+	
Narrow	1924	+	0	+	−	+	+	+	−	
*Wide	1925	+	0	+	0	+	+	+	−	
Narrow	1926	+	+	+	+	+	0	+	−	
(Wide)	1927	+	+	0	+	+	−	+	0	
(Wide)	1928	+	+	+	+	+	+	+	+	
Narrow	1929	+	+	0	0	0	0	0	0	Prev. fall dry
Wide	1931	+	+	+	+	+	+	+	+	
Narrow	1934	−	−	0	0	0	0	+	+	
Wide	1935	0	0	+	+	0	0	0	+	
*Narrow	1936	+	+	+	+	0	−	−	+	
Per cent +		63½	58	54	56	48	52	54	52	
Per cent 0		23	27	32½	31	35	23	23	21	
Per cent −		13½	15	13½	13	17	25	23	27	

were essentially like those shown in tables IV and V. The summaries of them, stated in per cent in exactly the same way, are incorporated in table VI along with the corresponding data from the two forest sites near Lake Cochituate. In this combined table, the five sets of correlations between growth and rainfall at the nearest stations are grouped to show differences or likenesses in the growth responses of hemlock and white pine.

The averages of the data for each period of the year (in bold-face type) show considerable variation between sites but on the whole a consistency in the growth response to the total rainfall of these specific periods. This is about equally true for the two species of trees. The means of these averages, computed across the table for the two species, are not so important for the ecological relations between water supply and growth because they ignore the significant differences between the averages of the correlations for the eight periods of the year. The mean averages were included in the table only to demonstrate the wide departure of the results from any that would be caused by chance correlations between growth rate and precipitation.

Briefly, the calculation of the percentages of chance agreement was based on the frequency of crests and troughs in the graphs of precipitation and ring widths, such as those in figure 4. Separate counts of them were made for the

TABLE V. *Walden Pond pine growth* vs. *Lake Cochituate rainfall*

+ = positive correlation
0 = no correlation
− = negative correlation

Width of ring	Year	May–July	May–Aug.	Apr. July	Apr.–Aug.	Mar.–July	Jan.–July	Jan.–Aug.	Preceding Sept.–Aug.	Notes
Wide	1860	+	+	+	+	+	+	0	−	
Narrow	1861	+	+	+	0	+	+	+	−	
Wide	1862	+	+	+	−	0	+	0	−	
*Narrow	1864	+	+	+	+	+	+	+	+	
*Wide	1867	+	+	0	+	0	0	+	+	
*Narrow	1870	+	+	−	−	−	−	−	−	
*Wide	1872	+	+	0	+	0	−	+	+	
Narrow	1877	0	+	+	+	0	+	+	+	
Wide	1878	−	0	+	+	0	+	+	+	
(Narrow)	1879	+	−	0	0	0	+	0	0	
Wide	1881	+	0	0	0	+	+	+	0	
*Narrow	1882	0	+	0	+	0	0	0	0	
Narrow	1890	+	+	+	+	0	+	+	+	
(Wide)	1891	−	0	0	+	0	+	+	+	
Narrow	1896	+	+	+	+	+	0	+	−	
*Wide	1897	+	+	+	+	+	+	+	0	
(Narrow)	1899	+	+	+	+	+	+	+	+	
(Wide)	1902	−	−	−	−	−	−	−	−	Prev. fall wet
Narrow	1904	+	+	−	0	0	0	0	+	
*Wide	1906	+	+	+	+	+	+	+	+	
Narrow	1907	+	+	0	+	+	+	+	+	
Narrow	1911	+	−	+	+	+	+	+	+	
Narrow	1912	+	+	−	+	−	−	0	0	
Narrow	1917	0	−	+	0	0	0	0	+	
Wide	1918	−	−	−	−	−	−	−	−	Prob. low run-off
Wide	1925	+	0	+	0	+	+	+	−	
Narrow	1926	+	+	+	+	+	0	+	−	
Wide	1927	+	+	0	+	+	−	+	0	
(Narrow)	1928	−	0	−	−	−	−	−	−	Dry till late May
(Narrow)	1931	−	−	−	−	−	−	−	−	
*Wide	1932	0	0	−	−	−	−	−	−	Prob. low run-off
Per cent +		68	61	48	58	42	52	58	42	
Per cent 0		13	19	26	19	23	19	23	19	
Per cent −		19	19	26	23	35	29	19	39	

TABLE VI. *Summary of positive, negative and zero correlations (in percentages) for white pine and hemlock growth rates in comparison with rainfall at nearby weather records stations*

Site	Correlation	May-July	May-Aug.	Apr.-July	Apr.-Aug.	Mar.-July	Jan.-July	Jan.-Aug.	Sept.-Aug.	Mean of Averages	Chance Averages
White Pine											
Bedford	+	59	59	36	51	38.5	44	51	62		15
Dedham		63	50	40	40	50	43	37	37		12
Walden Pond		68	61	48	58	42	52	58	42		12
Average		**63.3**	**56.7**	**41.3**	**49.7**	**43.5**	**46.3**	**48.7**	**47.0**	**49.6**	**13**
Bedford	0	10	15	41	26	28	28	23	15		70
Dedham		20	20	37	33	33	40	40	26		76
Walden Pond		13	19	26	19	23	19	23	19		76
Average		**14.3**	**18.0**	**34.7**	**26.0**	**28.0**	**29.0**	**28.7**	**20.0**	**24.8**	**74**
Bedford	–	31	26	23	23	33.5	28	26	23		15
Dedham		17	30	23	27	17	17	23	37		12
Walden Pond		19	19	26	23	35	29	19	39		12
Average		**22.3**	**25.0**	**24.0**	**24.3**	**28.5**	**24.7**	**22.7**	**33**	**25.6**	**13**
Hemlock											
Billerica	+	60.5	66	47.5	58	47.5	68.5	68.5	66		14
Natick		63.5	58	54	56	48	52	54	52		20
Average		**62.0**	**62.0**	**50.8**	**57.0**	**47.8**	**60.3**	**61.3**	**59.0**	**57.5**	**17**
Billerica	0	18.5	15.5	31.5	18.5	18.5	13	8	11		72
Natick		23	27	32.5	31	35	23	23	21		60
Average		**20.8**	**21.3**	**32.0**	**24.8**	**26.8**	**18.0**	**15.5**	**16.0**	**21.9**	**66**
Billerica	–	21	18.5	21	23.5	34	18.5	23.5	21		14
Natick		13.5	15	13.5	13	17	25	23	27		20
Average		**17.3**	**16.8**	**17.3**	**18.3**	**25.5**	**21.8**	**23.3**	**24**	**20.5**	**17**

several periods of the year and for the growth rates of each site and species. The graphs in figures 2 to 4 illustrate fairly the variations among them. In the right-hand column of table VI the probable chance relations are entered, averaged across the table for each site and for the positive, negative and zero correlations.

Only in the case of the negative correlations do some of the observed data come close to the chance possibilities. For positive correlations, the observed data are far above chance. For the absence of correlation between growth and rainfall, the observed data are well below chance. That observed negative correlations are somewhat above those predictable by chance for most periods of the year and for both pine and hemlock, is the only contradictory note in this general picture of a direct but imperfect response of growth rate to total precipitation for certain portions of the year. The contradiction is not serious though if attention is given to the results for the growing season rather than to periods with smaller percentages of positive correlations.

DISCUSSION

In view of the other variables in the tree's environment and of the inadequacy of total precipitation as a measure of water supply, these deviations from chance correlations in favor of positive correlations between growth and rainfall are so great that a cause and effect relation is a reasonable assumption. The chance that they are related through a third factor is remote. The lack of better consistency in the data, as summarized in table VI, is not surprising in view of the well known variation in weather records over short distances within the Boston Basin (Weber, '28). The same variations should be expected between forest sites and weather records stations when the distances are as much as 10 miles or in the case of the Milton station (at Blue Hills) with its higher elevation.

Of all the periods of the year that gave positive correlations in quantity, only eight seem worth reporting as possibly important in controlling water supply for growing trees. Two of them, April–July and March–July, are definitely below the others in percentages of positive correlation with growth and high in percentages of zero and negative correlations with the same. For reasons more or less obscure, the growth in subsequent months is not directly affected by the rainfall of March and April or else it varies roughly inversely with it. Probably for the same reason, the period April–August is of little significance in supplying water except as the hemlocks seem able to use the quantities that fall in August.

Leaving for a time the effects of fall and winter precipitation, revealed in the last three of the eight periods entered in tables IV to VI, the two periods that show the most direct connection with growth rate are May–July and May–August. In the averages of the positive correlations in table VI, these periods are clearly higher for both hemlock and white pine. Zero correlations are lowest of all the periods in white pine and average in hemlock. Negative correlations are very close to the chance allowance in hemlock though curiously high in white pine. Since the secondary growth of these two species probably begins in early May (Brown, '15; Lodewick, '28), the most important and consistent control of the growth increment is again shown to come through the growing season, as reported for northern New England (Goldthwait and Lyon, '37; Lyon, '36 and '40).

May to July inclusive is the decisive period for white pine both here and farther north with good evidence in the positive correlations of table VI for all three tree sites. The average of zero correlations for pine is equally good evidence and that for negative correlations is the lowest of all the periods, though still too high to be evidence for the point at issue. Detailed analysis of these negative correlations show them to be due to various factors, some of which can be seen in the data of table V, with the spacing and intensity of the rains an important point particularly at Dedham and Bedford. In other cases the rains came too late to stop drouth effects or the sub-normal precipitation did not mean a lack of water in the soil, due to water storage there.

For hemlock growth there is no choice in the data between May–July and May–August as the decisive period for water through rainfall. The notes in table IV suggest some additional effect of storage or lack of storage of water from the preceding fall, also noted in the unpublished table for Billerica hemlock and Lowell precipitation and reported previously for the species (Lyon, '36).

This effect of fall rains on growth rate in the following year may apply to white pine to some extent too but is not as regular a factor for either species as the rainfall of the growing season. The combination of the two periods gave fewer positive correlations with growth rate in critical years than any period considered here.

Finally there is the question of winter precipitation, for which the last three periods in tables IV to VI have some evidence. Hemlock appears to make more use of this water than does white pine, judging by the averages of the positive correlations. The more gentle slope at Billerica, with the higher percentage of agreement between hemlock growth rate and the precipitation in any period of the year that includes winter months, indicates that the relation of this water to that used by the tree later depends on low run-off as the snow melts. The same point is shown by the low percentages of positive correlations in the same three periods at Dedham, where the pine trees grew on a hill-top plot unlikely to retain its melt water. From this evidence and other comparisons between the data of table VI and the nature of the other three sites mentioned in it, it is probable that factors of exposure, topography and soil determine how much the winter precipitation affects the soil water supply in the Boston area.

In view of all the points brought out by the data for growth increment in relation to total precipitation measurements nearby, along with storage and lag effects from preceding seasons, it is probable that the year-to-year changes in the growth rates of these trees reflect closely the variations in their water supplies. The relative growth rates, at least in the "critical" years, measure this water supply factor better than do other records available to man. This is one more demonstration of the point that apparently holds for many localities from the Pacific Northwest (Keen, '37) to northern New England (Lyon, '36).

From the agreement in the dates of minimum and maximum growth rates at the several sites named in tables II and III, it follows that the years of drouth and abundance are usually the same within the Boston area. The exceptions usually come at sites like Manchester near the Cape Ann shore and Douglas so much farther inland. In many cases they fail to appear in a record because the trees are less sensitive to environmental changes at that period, as in the old pines at Carlisle.

If a long sequence of ring width is available for any problem of dating wood of uncertain age, the cross-dating between timbers of the same species is probably accurate enough for careful use of the method in the area. From the comparative dates for hemlock in table II, it is doubtful though if cross-dating is possible between New Hampshire wood and that grown near Boston. The general drouths and years of abundant water supply are the same but each area has its own dates for local effects, such as 1852, 1864 and 1926 for Boston drouths as recorded by both pine and hemlock. In a single case of cross-dating, it would be impossible to identify them and impractical to make allowance for them.

That cross-dating must be confined in most cases to wood from the same species of tree and within a limited area, though many drouths and good years are registered throughout a broader area, is due in part to the local water supply conditions and in part to the differences in the sequence patterns of minimum and maximum growth increments for two species. Hemlock and white pine are both sensitive to changes in water supply, with hemlock probably a more reliable indicator because its rings are seldom "complacent" in the matter of width from year to year. As shown in tables II and III, there are probably more years of agreement in dates between the two species near Boston than years in which only one of them indicates a good or poor year for sites some miles apart. It is difficult to determine why the species differ so in these years of non-agreement but the general agreement is more important. It indicates years that are definitely lacking in or well supplied with water for the growing seasons of the species. Minor differences in their growth periods must account for many of the others. Direct or indirect effects of temperature may be responsible for others, modifying the response to the water present. Lag effects at some sites, as noted in table IV, would explain other discrepancies and help to emphasize the dependence of growth rates of both species upon the water available to their roots.

SUMMARY

Using large trees felled in the Boston area by the hurricane of 1938, trunk sections were taken from seven stands of white pine and four lots of eastern hemlock trees. The widths of annual rings

of wood were averaged for each year at each site and used as indices of growth rates. From the agreement among the four graphs of hemlock growth increments, the years of maximum and minimum growth rates for the area were determined. A similar set of dates was read from the crests and troughs of the seven graphs for white pine ring widths. Comparison of the relatively high or low growth rates in these years with the rainfall records from official stations near the forest sites brought out the importance of rainfall during the growing season. There was also some evidence of lag and cumulative effects from previous seasons and a general demonstration that fluctuations in growth rates from year to year reflect the variations in water supplied through the soil.

Because the years of drouth and the years of abundance are essentially the same throughout the Boston area, though with some differences in the sequences for hemlock and white pine, cross-identification between timbers of a species is sufficiently accurate for use of the method in dating wood of uncertain age contemporary in part with dated wood. Cross-dating between the trees of the Boston area and those of New Hampshire is not possible, however, because each area has its own dates for local drouth and abundance effects in addition to the years of widespread drouth or water abundance recorded by the growth increments from both areas.

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RESPONSE OF THE ANT PRENOLEPIS IMPARIS SAY TO TEMPERATURE AND HUMIDITY CHANGES

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The surface activities of the ant *Prenolepis imparis* Say have attracted the writer's attention during three years of collecting because of certain peculiar traits in which they differ from other ants. In the autumn the workers swarm on fallen fruit and their nests are conspicuously marked with circles of excavated yellow clay, but in the summer the ants and their nests seem to disappear entirely. Moreover, the workers seem always the first ants out in the spring and the last to be walking about in the fall, and a period of winter collecting showed that they may be out during any month of the winter. A detailed study of the species for purposes of population counts (Talbot, '43) led to a conjecture that temperature or relative humidity changes might account for the fluctuations in above ground activity.

It was found that the ants did react to temperature to a remarkable degree and to humidity to a less but still discernible amount. The problem was to keep records of the number of ants above ground at various times to see if their numbers fluctuated in correlation with temperature and relative humidity changes. No way was found of ascertaining the total number of ants outside the nest at a given time. Arbitrarily it was decided to count the number of ants to be seen within a radius of 3 inches of each nest entrance. This technique was very accurate when few ants were out but became progressively less accurate as activity increased and ants foraged out into the surrounding territory. Therefore any differences in number of ants counted is conservative and the true differences are even greater than shown.

Ants were counted four times a day (at approximately 7:30 A.M., noon, 5 P.M., and 10 P.M.) and at these times temperature and relative humidity were recorded with a psychrometer (Julian P. Friez and Sons, Inc.) so constructed that a current of air can be blown over the wet and dry bulbs while they are standing 2½ inches above the ground. Records were taken at intervals, during the winter, to determine the lowest temperature at which the ants can forage; in the spring, to follow preparations for flight and the subsequent decline of activity; and in midsummer to observe maintenance of, and emergence from, the summer lull. Each record involved the total count of all the ants at ten nests since colonies varied so much in activity that a quantitative study was necessary. During the winter and spring ten nests located at St. Charles, Missouri, were studied and for summer work ten similar colonies at Tiffin, Ohio, were used. Both of these sets of colonies had been studied previously and were known to be flourishing.

Table I and figure 1 give a summary of all the winter and spring records (441 in all) taken between the temperatures of 31° and 90° F. at St. Charles, Missouri. From this table it can be seen that *Prenolepis imparis* workers appear above ground at extremely low temperatures. They begin to emerge as soon as the temperature reaches above freezing, and they increase in numbers as temperatures rise until they reach a peak between 45° and 65° F. Above this there begins a decline which becomes progressively greater as temperatures rise until above 85° F. surface activity has practically ceased. This preference for cold weather has been observed before by Burrill (reported by Wheeler, '30) who found the ant out at temperatures of freezing or a little below. Wheeler states that this win-

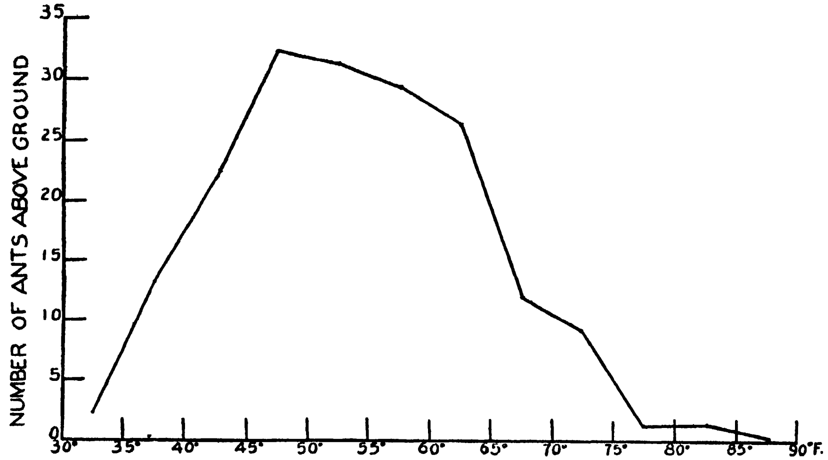

Fig. 1. Showing the temperatures at which *Prenolepis imparis* workers are most numerous above ground. (See table I.)

ter activity, plus early spring nuptial flight, and the habit of nesting in poorly drained soil in the shade, all indicated that *Prenolepis* is essentially negatively thermatropic in contrast to our common local ants which are distinctly thermophilous. Wheeler further states that it belongs to the "preglacial circumpolar fauna" and is "almost indistinguishable from *P. henschei* Mayr, a species that flourished in the amber forests of the Lower Oligocene Tertiary of northern Europe."

Winter.—Observations during the winter show that some *Prenolepis* leave the nest whenever the temperature permits motion. This begins at approximately 32° F. At these low temperatures the ants walk slowly or stand quietly near entrances; as it becomes warmer more and more ants emerge, move faster and begin to forage for food. Occasionally an ant is trapped out by a sudden drop in temperature before it can get back to the nest and lies all night at below freezing temperatures, unable to walk but capable of moving legs and antennae slightly. (Ants have been seen at each of the following temperatures: 21.5°, 28°, 29°, 30° F.) When the ground becomes frozen there is a delay in emergence until it begins to thaw.

During the first few days of cold weather in the fall dead ants are found thrown out at almost every nest entrance, but no such dead ants are found later in the winter or in the spring. Almost no excavating is done during the winter but nest entrances are kept open at all times.

Although ants are above ground at any time during the winter when the temperature is above freezing, active foraging begins about 35° or 40° F. This foraging is not very profitable during late winter but in the early winter just after the first frosts there is a great spurt of foraging because many insects and other small animals are killed. Aphids, leafhoppers, parts of crickets and grasshoppers, spiders and centipedes, earthworms, etc., add meat to a diet which has consisted almost exclusively of fruit all fall. In the winter when the temperature reaches freezing or below at night and rises during the day the ants are almost exclusively diurnal, a few beginning their morning activity as soon as the temperature rises above freezing and a few staying above ground until freezing is reached again.

Thus *Prenolepis* has no real hibernation period. This is quite in contrast to the other ants of the region. In the winter of 1940–41 other ants are just finishing their hibernation preparations when the first frost occurred at St. Charles (Nov. 7) and were not seen after this date. (*Lasius niger americanus* Emery, *Formica fusca subsericea* Say and *Monomorium minimum* Buckley were present in the orchard). The following spring *Lasius* and *Formica* were first seen on April 7 actively digging out and next day their craters were conspicuous in the orchard. Two days later the first *Monomorium* were making their little craters. Thus in the winter of 1940–41 the hibernation period for these ants extended from Nov. 7 to April 7, a period of 5 months.

Spring.—Spring activities, prior to the nuptial flight, are almost entirely directed toward modification of the upper parts of the nest. This modification consists of vigorous excavation in which entrances are multiplied (by flight time they range from 2 to 7) and a series of extra chambers are dug out just below the ground surface which serve as a loitering place for the males and females. During these early spring days little circles of yellow clay soil accumulate around nest entrances, making them conspicuous spots in the grass. Foraging is continued but it is now subordinated to the excavation activities.

In 1941 flight preparations were elaborate and long drawn out. They began March 21 and continued until April 6. On March 21 the temperature reached the 60° F. level for the first time and a group of males were discovered clustered together under the dried leaves which overlaid a nest. On March 23 (noon temp. 73° F.) the first males were seen out in the open, all staying very near to, or down in, nest openings. From then on a few males came out for a short time during the middle of each day but made no attempt to move far from the nests nor to leave the ground. Temperatures ranged from freezing at night to 47° or 50° F. at noon. On March 31 activity was speeded up (noon temp. 61° F.) when 41 males were counted on the plot of ten nests and the first females were seen. Some of both males and females were now moving away from nest entrances and were hiding beneath leaves and grass. Several females were climbing up and down grass stems. Workers were very busy excavating and there was such a general activity that flight seemed imminent, but nothing happened and by 5 P.M. the males and females were all back in the nests. It seemed likely that flight would occur next day, but there followed five days of gray, rainy, cool weather (noon temp. 47° to 63° F.) when there were very few males or females above ground. These were out only during the middle of the day and were usually all below ground by 5 P.M. At this time several dilatory males were seen being pulled into entrances by workers, but at all other times workers went about their business of excavation and paid no attention to the winged forms.

April 6, the first day of flight, dawned clear, though chilly, and at 7:30 A.M. a number of males were already at the surface and by 10 o'clock (temp. 62° F.) great numbers of them were coming out of the multiple nest openings and clustering in groups in the dead leaves. By this time the sky was overcast and hazy and there was alternate sunshine and

TABLE I. *Showing the temperatures at which* Prenolepis imparis *workers are most numerous above ground.* (See fig. 1)

Temperature	Mean no. of ants seen at each observation*	No. of observations
31°–35° F.	2.32	34
36°–40° F.	13.34	55
41°–45° F.	22.69	42
46°–50° F.	**32.65**	52
51°–55° F.	**31.70**	51
56°–60° F.	**29.93**	49
61°–65° F.	**26.72**	47
66°–70° F.	12.10	38
71°–75° F.	9.42	35
76°–80° F.	1.38	13
81°–85° F.	1.40	15
86°–90° F.	0.40	10

* Each figure given is a mean of the total count of 10 colonies at each observation. Ants were counted within a radius of 3 inches of each nest entrance. Records were made during the months of November, December, January, February, March, April, and May.

clouds for the rest of the day. At 11 A.M. (66° F.) a few females were emerging and the males were spreading out further into the grass. At 11:30 the first males were seen to fly and within 7 minutes many ants were flying and mating. Males climbed blades of grass and took off readily so that shortly there were swarms of them flying above the grass. The much larger females were not so successful at flying. They would climb up grass stems, spread their wings and then fall back or, at best, fly only a short distance. A few succeeded in flying higher (one was seen above the apple trees) but the majority never did more than fly a few inches or feet and then drop back to earth.

At the height of flight there was much activity in the orchard with swarms of males taking off from the nests and flying just above the grass. Winged females were making their bungling attempts at flying. Recently dealated females were running about and numerous workers were excavating and foraging but were not taking any part in the flight. The peak was reached between 12:30 and 1 P.M. (73° F.) although there were still many ants in the air at 2 o'clock. At 3 o'clock (71° F.) flying and mating were still occurring, but by this time some males and females were going down nest entrances and in several places workers were seen pulling males into the nests. At 4 P.M. (66° F.) flight was definitely over for the day with only a few males lingering at nest openings.

Next day (4–7–41) was hazy and gray and, although many males and a few females were outside the nests, none were seen to fly and all were back in the nests by 5 P.M. The following day was still dull, with a threat of rain, and again males and females were out but did not fly. But on the third day (4–9–41), with intermittent sun, there was a sparse flight during the middle of the day (noon temp. 67° F.). Next day (noon temp. 70° F.) flight was more general and was similar to that of the first day although it did not in any way approach it in magnitude. Thus in 5 days there were 3 days of flying. No more winged *Prenolepis* were found in the orchard and the dealated females had dug down beneath the surface and disappeared.

The records of temperature and relative humidity kept from March 23 until after the flight showed that flight occurred on the first warm, sunny day of spring, following a period of rain and high humidity. After the first day, flight was interrupted by two cool, cloudy days but was resumed for two more sunny days. The three days of flight cleared the nests of all males and females.

In 1942 flight was earlier and much less conspicuous. On Feb. 27, when records were begun, spring excavations had not yet started. They began about the first of March although there were still patches of snow in the orchard. This year not so many nest entrances were made (they averaged 2.70 per nest at flight time). The first males were seen March 11 (noon temp. 55° F.). On March 15 the weather suddenly turned very warm and a number of males were out and much excavation was going on but no females were yet seen. Next day flight occurred. The morning had been cloudy and there was a short sudden rain but at noon the temperature reached 80° F. in the sun and flying activities were getting under way. By 1 P.M. matings were occurring and by 3 P.M. flight was about over for the day, although at 5 o'clock there were still a few males on the wing. At this time a worker was seen to carry a male back into the nest. Next day the temperature never reached above 43° F. and the following days were also cool. On March 23 and 25 there were two very sparse flights which cleared the nests of winged forms for the year. (Noon temperatures were 69° and 74° F.)

The 1942 flights had been less spectacular and less well prepared for than those of 1941 and they were also earlier. But if spring progress is to be considered instead of dates the two flights were at about the same time. For instance, in

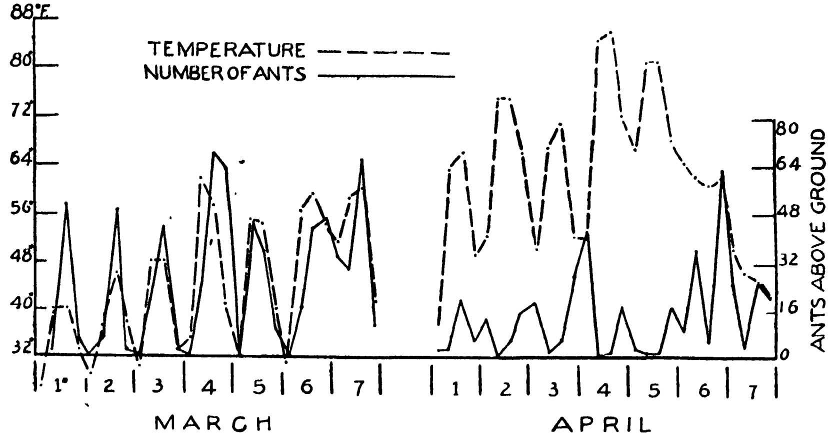

FIG. 2. Comparison of activity of *Prenolepis imparis* for the first week of March and the first week of April 1942. In March the temperatures were favorable for activity during the day while in April they ranged above the optimum.

* The first 7 days of March and April. The 4 points for each day represent temperatures recorded at 7:30 A.M., 12 noon, 5 P.M., and 10 P.M., and the ants seen at these times.

1942 pink magnolias and apricots began blooming March 23 (the second day of flight) while in 1941 they began April 10 (the third day of flight). Each year flights occurred just after the peach, plum, and pear trees bloomed. Each year *Formica, Lasius* and *Monomorium* were just ending hibernation.

Spring excavations ceased after flight except when rain required the reopening of entrances. Only one colony continued to dig during the later spring and it must have enlarged its nest considerably. This was evidently a small colony because it was the only one of the ten which had no males and females.

The ants did little foraging during the spring. *Prenolepis* workers were seen attending aphids, foraging on a dead Mayfly and June-beetle and bringing in small insects, but at no time were many ants involved. They kept entrances open but as excavation ceased grass and weeds grew over them and there was nothing visible of the circle of clay pellets which formerly marked their place.

Figure 2 shows the fluctuations of temperature and of ants recorded four times a day for the first week in March and the first week in April. These are samples of records kept during the winter and spring, selected because they show the contrast in periods of activity when temperatures are constantly touching freezing at night and were fluctuating up from this through a favorable range (March 1–7), and activity when temperatures are constantly fluctuating higher than the optimum during the day (April 1–7). It will be noticed that in March the ants were almost entirely diurnal because optimum temperatures came at midday while in April they were primarily nocturnal because day temperatures were too high. This tendency to work mainly at night during warm weather may explain why Wheeler ('30) and Wesson ('40) considered them predominantly nocturnal.

Summer.—It was found that as spring progressed foraging dwindled at all temperatures and the tendency to stay in the nest became stronger and stronger. Table II and figure 3 show this for March, April, and May of 1942. It will be seen that at like temperatures there is increasingly less activity. However it will also be noted that the peak of activity still comes at the cool temperatures (40°–

TABLE II. *Showing the decline in numbers of* Prenolepis imparis *workers above ground during the spring months.**
(See fig. 3)

Temperature	March		April		May	
	Mean no. of ants counted	No. of records	Mean no. of ants counted	No. of records	Mean no. of ants counted	No. of records
36°–40° F.	17.16	24	10.75	4	—	—
41°–45° F.	28.22	18	23.33	6	—	--
46°–50° F.	41.26	15	18.85	7	13.60	5
51°–55° F.	34.50	12	22.30	10	11.28	7
56°–60° F.	36.27	11	22.33	9	7.57	14
61°–65° F.	45.44	9	18.14	14	8.82	17
66°–70° F.	—	—	10.58	12	4.95	21
71°–75° F.	—	—	4.80	10	2.00	20

* Each figure given is the mean of the total count of 10 colonies at each observation. Ants were counted within a radius of 3 inches of each nest entrance.

65° F.) with a sharp drop off below and above this range.

In May fewer and fewer ants were coming out of the nests, even at favorable temperatures and some colonies had almost ceased to emerge. Some colonies had only 5–7 ants recorded during the entire last two weeks of May while others had as many as 34–44 during this period. Aestivation was beginning but was still not quite complete on June 1 when observations had to cease at St. Charles.

No records were kept in June but on July 2 a similar set of observations (4 times daily) was begun on a similar set of ten nests at Tiffin, Ohio. Casual observations of these nests had shown a few ants out during the early part of June but none at all were seen during the last two weeks of June, although they were looked for. Records from July 2 to July 16 show only one ant (on July 14) seen in all the 55 observations although 13 records were below 65° F. (when a mean of one ant at each nest might have been expected) and 25 were between 66° and 70° F. (when a mean of one ant at each ten nests might have been expected). Thus there existed a complete aestivation during which ants remained in the nest no matter what the temperature.

Just as there was considerable irregularity shown by the various colonies in entering upon this lull so coming out of aestivation also varied considerably. The first ants amerged from the ten nests the following dates: 7–14, 7–16, 7–25, 7–31, 8–4, 8–7, 8–9, 8–11. Thus the aestivation period lasted 4 weeks or more for the first out and 8 weeks or more for the last. This corresponds to records made in 1941 (Talbot, '43) in which 15 colonies spread their emergence from July 19 to Aug. 31. *Prenolepis* matures its larvae during this summer lull, evidently feeding them with the honey stored in the repletes. By the end of summer repletes have dropped from approximately 80 per cent to about 67 per cent of the workers and the whole colony must be at a low ebb of nutrition.

The time of emergence from aestivation corresponds roughly to the time of maturing of fruit in the orchard when any bit of fruit found is devoured quickly by the ants. That it is not the presence of fruit that determines the breaking up of aestivation can be shown by the fact that fruit distributed during the first part of July brought no response whatsoever. Evidently there were not even scouting ants above ground at this time.

Once the summer lull is over and ants are foraging for food the response of any particular colony depends primarily upon

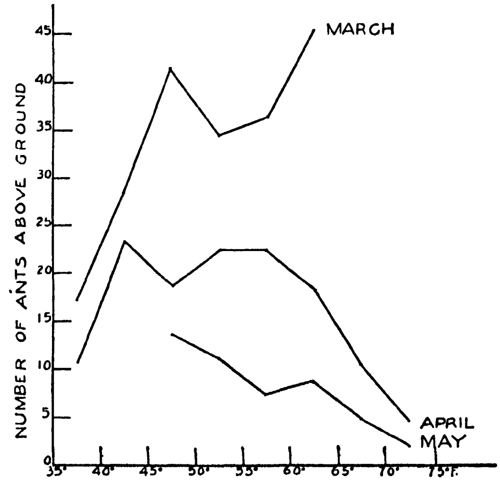

FIG. 3. Decline of above ground activity of *Prenolepis imparis* during March, April, and May. (See table II.)

the food found. Thus a colony has been known to maintain 5 to 10 workers on a piece of fruit through temperatures as high as 87° F. Other colonies which had not found fruit were entirely dormant at this time.

Other kinds of stimuli, such as excavation activity or preparation for flight, may keep the ants out at unfavorably high temperatures and individual colonies vary greatly in the numbers of workers which emerge above ground. Response to temperature is evidently a population phenomenon which is not necessarily adhered to slavishly by individual ants or by individual colonies at all times.

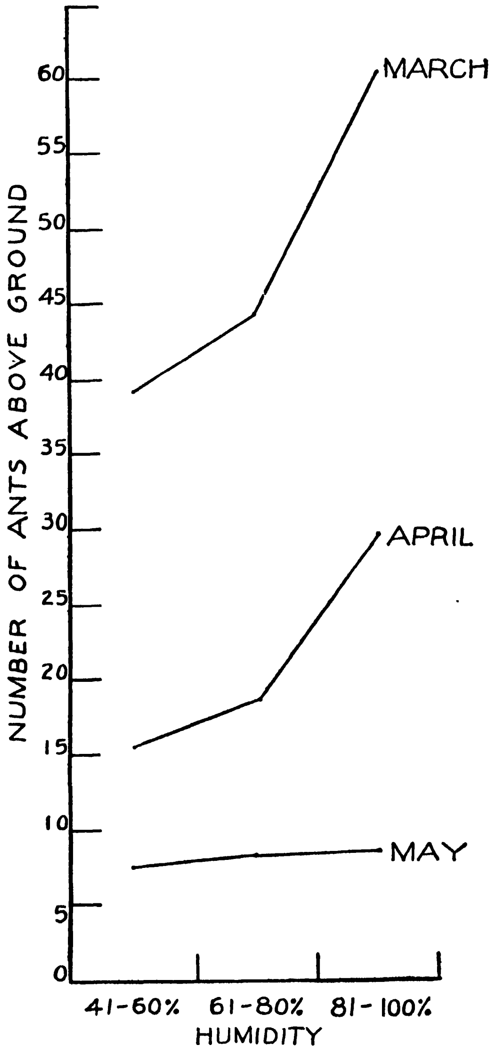

Fig. 4. Response of *Prenolepis imparis* to high relative humidity at temperatures between 46° and 65° F. (See table III.)

Table III. *Showing response of* Prenolepis imparis *to high humidity at temperatures between 46° and 65° F.** (See fig. 4)

	41% 60% humidity		61%-80% humidity		81%-100% humidity	
	Mean no. of ants counted	No. of records	Mean no. of ants counted	No. of records	Mean no. of ants counted	No. of records
March	39.10	20	44.58	17	61.50	6
April	15.60	10	18.78	19	29.60	10
May	7.77	2	8.28	15	8.54	24

* Each figure given is the mean of the total count of 10 colonies at each observation. Ants were counted within a radius of 3 inches of each nest entrance.

Whenever temperature records were taken relative humidity was also recorded. It was obvious from casual observation that high humidity favored activity, for the ants were always unusually busy after a rain and were also out during the rain unless it was a continued downpour. However, no direct correlation could be made between activity and relative humidity without first considering temperature, for always the main reaction was to temperature. For example, there would be few ants out at high humidity at 75° F. in comparison to those out at high humidity at 55° F. So reaction to relative humidity was calculated for temperatures between 46° and 65° F. when activity is at its height. Within this range of temperatures there can be shown a direct correlation of increased activity with high relative humidity. (See table III and figure 4.) It will be noticed that in May reaction to favorable humidity was dying out just as reaction to favorable temperature was.

All of these results were obtained by grouping the records of 10 colonies. When the results for each colony were separated it was found that, while colonies differed in the amount of activity, yet the reaction to temperature and humidity was essentially the same for each colony.

SUMMARY

1. *Prenolepis imparis* is a cold weather ant, beginning activity above ground at temperatures just above freezing and reaching its peaks of foraging at temperatures between 45° and 60° F. Above 60° there is a decrease in numbers of ants above ground which progresses steadily with rising temperatures until, above 75° F., almost no ants are found above ground.

2. *Prenolepis* has no definite hibernation period and individuals will forage during the winter whenever temperatures allow movement (the ants can move slowly at 32° F.). In contrast, there is maintained a midsummer aestivation period of from one to two months in which no ants appear above ground even though temperatures are favorable.

3. Flight of males and females occurs on the first warm days of spring when other species of ants are just finishing hibernation.

4. *Prenolepis* responds positively to high humidity and, during favorable temperatures, reached peaks of activity at humidities of 80 per cent to 100 per cent.

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THE DISTRIBUTION OF SOME IMPORTANT FOREST TREES IN CANADA

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Introduction

Knowledge of the range of a particular tree species serves many useful purposes; the addition of details of its relative abundance within that range would greatly enhance this usefulness. Such information is not only valuable from either a silvicultural or a utilization standpoint, but is of prime importance in estimating the potential spread of host-specific insect or fungal attacks, with a view to organizing remedial measures.

Certain elements of this information can be derived from range maps, forest cover maps, and ecological studies; also from more comprehensive works such as life-zone or regional classifications of forests (Halliday, '37). To obtain a complete picture, however, consideration of the quantitative values given by forest survey and inventory is indispensable.

The present paper is an attempt to synthesize a picture of the varying relationships of certain tree species, within the limits of their range, to the mass of the other tree species present. The basic data on which it rests were compiled and worked up into maps[1] by the second of the co-authors, for the original purpose of providing a background for forest insect survey work. It should be stressed that the maps thus obtained are necessarily restricted to the area within the boundaries of the Dominion of Canada.

Detailed basic data were fortunately available in the recently published forest inventories for British Columbia (Mulholland, '37) and New Brunswick (Morison, '38). Permission was kindly given for the use of interim figures for a forest inventory of Quebec. For the other provinces, although more generalized figures have been published for Ontario (Sharpe and Brodie, '31) and the Prairie Provinces (Harrison, '36), references had to be made to individual cruises and forest surveys.

The authors wish to record their sincere appreciation for assistance given and information communicated to them by J. F. Sharpe and H. H. Parsons of the Ontario Department of Lands and Forests; D. Roy Cameron, Dominion Forester; J. E. Guay, Director of Inventories, Quebec Forest Service; E. E. Shaw, Canadian International Paper Company, Montreal; R. S. Johnson, Mersey Paper Company, Liverpool, N. S.; and D. W. Jamer, the James McLaren Company, Buckingham, Quebec.

Grateful acknowledgment is also made to Dr. C. C. Heimburger and A. E. Porsild for their kindness in critically reading the manuscript, to D. A. Nichols, Bureau of Geology and Topography, for his valuable assistance in connection with the map of Pleistocene glaciation; and to H. A. Raizenne, Division of Entomology, for making the drawings for the plates.

Method

The method employed, in brief, was the calculation from volume figures of the percentage stand composition, for unit areas surveyed, of the constituent tree species. This area is practice varied from

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[1] The detailed maps resulting from this compilation are deposited with the Forest Insect Investigations Unit, Division of Entomology, Department of Agriculture, Ottawa.

100 to 1000 square miles in size. From such data the abundance in relation to other species found in the unit area, or the relative population intensity for a given tree species within its range, could be determined.

There are some disadvantages inherent in this method. First, the relative volume of a species on a given area will change as the stand matures or is affected by cutting, fire, or destructive insect or fungus attacks. Most of the volume figures date from between 1925 and 1935, although some surveys as early as 1910 had to be used. This source of error is compensated, to some extent, by the final use of only three broad population intensity classes. Secondly, the result will be influenced by the size of the sample area. If this is large, a close approximation to the average conditions in the surrounding country should be obtained; if it is small, there exists a possibility that the distribution of species found thereon will not be respresentative.

In interpreting the maps, it must be borne in mind that the prominence of a given species in any one area is affected by the number of other species and their volume in that area. The maps can indicate only relative abundance, not actual abundance. It is conceivable that an area of low actual abundance of a given species may show a high relative abundance due to the scarcity of other species (by default, as it were), as for instance occurs in the case of spruce in the far north. For this reason the authors have endeavoured to interpret the maps with caution. Another point to be noted is that the specifications for the three broad population intensity classes are not the same for every species, but have been set on the scale suitable to the character of the species concerned.

The authors feel that, in spite of such shortcomings, the method followed is one calculated to give as accurate and generally true a picture as can be derived, and that it is the best means whereby such designations as "balsam country" or "yellow birch highlands" can be substantiated on a quantitative basis. In this respect, the present work may be considered as a complement to *A Forest Classification for Canada* (Halliday, '37).

ORGANIZATION OF DATA

Cruise or inventory figures were obtained for a unit area, e.g., a drainage basin, group of townships, park, forest reserve, cutting area, or timber limit. The most convenient size for such areas was found to be from six to twelve townships. Figures for all tree species were reduced to the same unit of volume, whether cords, cubic feet, or board feet, and totalled; the volume of each species was then calculated as a percentage of the total volume. The geographical boundaries of the unit area concerned were plotted on a key map, 16 miles or 35 miles to the inch, and the percentage figures noted thereon.

Each tree species was then assigned to a 35-mile to the inch map, on which were drawn the boundaries of all the unit areas covered. The percentage figures were divided into ten size-classes, the limits of each class being decided by the extreme quantitative range for the particular species. Colors, arranged in a series similar to that used for contour maps, were assigned to each class, and the unit area tinted accordingly.

The result thus obtained may be considered as a 'contour' map of the population density of the particular tree species, although a certain amount of interruption in the 'contours' was inevitable. These unit surveys gave a coverage of at least 85 per cent of the area of merchantable timber in Canada, being complete in British Columbia, Quebec and New Brunswick, but comprising only 70 per cent of the total area in the Prairie Provinces and Ontario. From these ten size-classes, three broad divisions of population density (light, medium and heavy) could be derived with ease and accuracy.

The limits of geographical distribution

have been determined from the latest data available. The lack of information from the extreme northwest of the Dominion still remains a serious drawback. Difficulty was experienced, in the case of some species, in determining the limit of continuous distribution as contrasted with sporadic occurrences. In most cases it was found feasible to indicate isolated outliers on the map, though many small ones and all those in the far north have of necessity been omitted.

Relation to Forest Geography

A study of the maps also stimulates thought on the whole question of the reinvasion of the Canadian land-mass by forest flora in interglacial periods, and in particular following the last or Wisconsin glaciation. Considerable light has been thrown on the matter by a number of studies, now available, based on bog pollen distribution analyses.

No attempt will be made to deal with opposing theories as to what happened to the forest formation in face of the advancing ice, but the authors now incline to the view of Hultén ('37) and of Raup ('41) that there is reason to believe that the bulk of the tree vegetation was destroyed and not forced south by the ice. Certainly, existing ice-sheets in their advance impinge directly on mature forest vegetation and destroy it, as on the Alaskan coast (Cooper, '42); and the impossibility of sufficiently rapid retreat, together with the effect of drying winds from anticyclones over the ice-sheets, would be strong factors in this destruction. Moreover, the possibility must be borne in mind that the ice-masses, originating as they are considered to have done at points in the interior of the continent, would impinge directly upon the forest itself at that time, rather than upon land already denuded of forest.

For re-invasion four main forest biotas were available. The eastern biota was centered on the Appalachian land-mass, being mainly a mixed forest containing maples (*Acer* spp.), yellow birch (*Betula lutea* Michx.), oaks (*Quercus* spp.), large-toothed aspen (*Populus grandidentata* Michx.), and other deciduous trees; and white pine (*Pinus Strobus* L.), red pine (*P. resinosa* Ait.), jack pine (*P. Banksiana* Lamb.) eastern hemlock (*Tsuga canadensis* (L.) Carr.) balsam fir (*Abies balsamea* (L.) Mill.) and red spruce (*Picea rubra* Link.). The western biota, situated beyond the former Cretaceous depression of the center of the continent, and centered on the Cordilleran land-mass, was predominantly coniferous, with such species as Douglas fir (*Pseudotsuga taxifolia* (Lamb.) Brit.), western white pine (*Pinus monticola* Dougl.), ponderosa pine (*P. ponderosa* Dougl.), grand fir (*Abies grandis* Lindl.), Engelmann spruce (*Picea Engelmanni* Engelm.) and western larch (*Larix occidentalis* Nutt.).

The third or boreal biota, containing such species as white spruce (*Picea glauca* Voss), black spruce (*P. mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) Koch), is considered by Hulten ('37) to have centered around the Bering Sea. The position of such boreal species as trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), lodgepole pine (*Pinus contorta latifolia Engelm.*) and alpine fir (*Abies lasiocarpa* (Hook.) Nutt.) is not clear, although evidence points to a main center in the Yukon Valley.

A fourth element, containing Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* D. Don.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes), all typical of the Pacific Coast, may have an association with the southern part of the Bering Sea area.

The treatment of this subject, specifically of the arctic and boreal biotas, by Hultén is most significant. His principal contribution lies in his recognition of centers of population from which boreal species have spread progressively over the

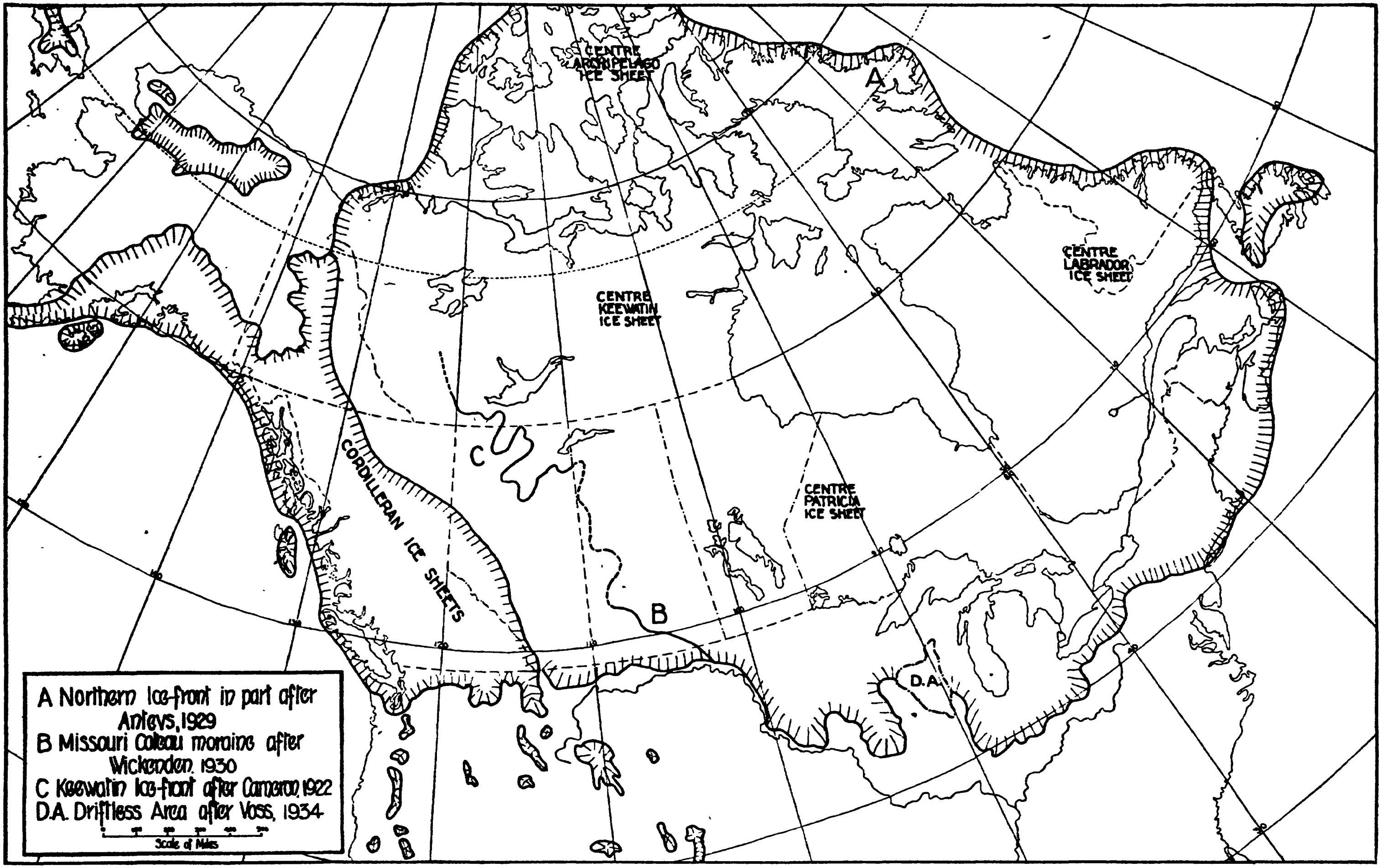
CENTRE ARCHIPELAGO ICE SHEET
A
CENTRE LABRADOR ICE SHEET
CENTRE KEEWATIN ICE SHEET
C
CORDILLERAN ICE SHEETS
CENTRE PATRICIA ICE SHEET
B
D.A.
A Northern Ice-front in part after Antevs, 1929
B Missouri Coteau moraine after Wickenden, 1930
C Keewatin Ice-front after Cameron, 1922
D.A. Driftless Area after Voss, 1934
0
Scale of Miles

FIG. 1. Map of Wisconsin glaciation in North America. (Compiled with the assistance of D. A. Nichols, Bureau of Geology and Topography, Canada.)

Northern Hemisphere. By the superimposition of the ranges of a large number of boreal plant species, centers of gravity (centra) were found to lie in the lands bordering the North Pacific, especially in Manchuria, northern Japan, Kamchatka, and the region around the Bering Sea (northern and southern Beringia), all within areas not covered by Pleistocene ice.

From the centra in Beringia then, boreal species spread as "radiants" into North America as a whole, reaching the Atlantic Coast by at least the time of the D-interglacial (Yarmouth) period. They were able to survive the two subsequent glaciations, the Illinoian (or maximal) and the Wisconsin, mainly in refugia adjacent to the ice-sheets. These refugia, from which the flora again populated the land as it was freed from the ice, were located principally along the Atlantic continental shelf (exposed at that time by recession of the sea), the southern fringe of the ice-front (notably to the south of the Great Lakes), and the valley of the Yukon River.

The capacity of species left in refugia to repopulate the land-mass was modified by the vicissitudes they had undergone. Those species which were depauperated as to biotypes, and thus as to potential variability, are considered as "rigid" species, and are likely to be found in the vicinity of their original refugia at the present time; while others, more fortunate in retaining their biotypes, are termed "plastic" species, and are those that have been able to recolonize large areas in postglacial times.

While it is conceded that the Illinoian and the Kansan glaciations were the most severe in their effects, it is the extent of the last, or Wisconsin, which principally determines the present distribution pattern of the constituent tree species of the forest; it is therefore shown on the attached map (figure 1), compiled mainly from information contributed by Antevs ('29), Wickenden ('30), Cameron ('22) and Voss ('34). Present opinion considers that, during the Wisconsin glaciation, ice advance and recession took place from a number of centers, the main weight of which shifted gradually from east to west. From centers in the interior of Labrador, in the Patricia district of northwestern Ontario, and in the Keewatin district of the Northwest Territories, there was progressive radiation of ice-sheets so that, at one time or another, the entire Laurentian shield was over-run, and ice had reached east to the Atlantic, south to the Mississippi and Ohio Valleys, north over much of the Arctic Archipelago, and westward towards the Rocky Mountains. The Cordilleran ice-sheet, probably arising from a number of centers on the western mountains, spread west to the Pacific, south into the State of Washington, northwest around the Yukon Valley and eastward towards the Mackenzie Valley.

SPRUCE

This tree genus may be considered the most important in Canada, making up as it does as much as 37 per cent by volume of the total timber resources of the Dominion. Two species, the white and the black spruce, are characteristic trees of the boreal forest, extending to the northern limit of forest, and forming an ever-increasing percentage (up to 99 per cent) of the total stand as the other species drop out (figure 2).

The northern limit of spruce corresponds very closely with the July isotherm of 10° C. (50° F.) in Ungava. West of Hudson Bay, however, it recedes to the southward of this isotherm (see figure 3, taken from Brooks and Connor, '36). The country in these parts is characterized by outliers of forest extending far down the northern rivers, together with scattered clumps of dwarfed ("bush") spruce in the intervening lands. Similarly, the southern limit of the belt of heavy spruce (forming over 60 per cent of the total stand) follows roughly the July isotherm of 18° C. (64° F.) over the Laurentian Shield; this correlation

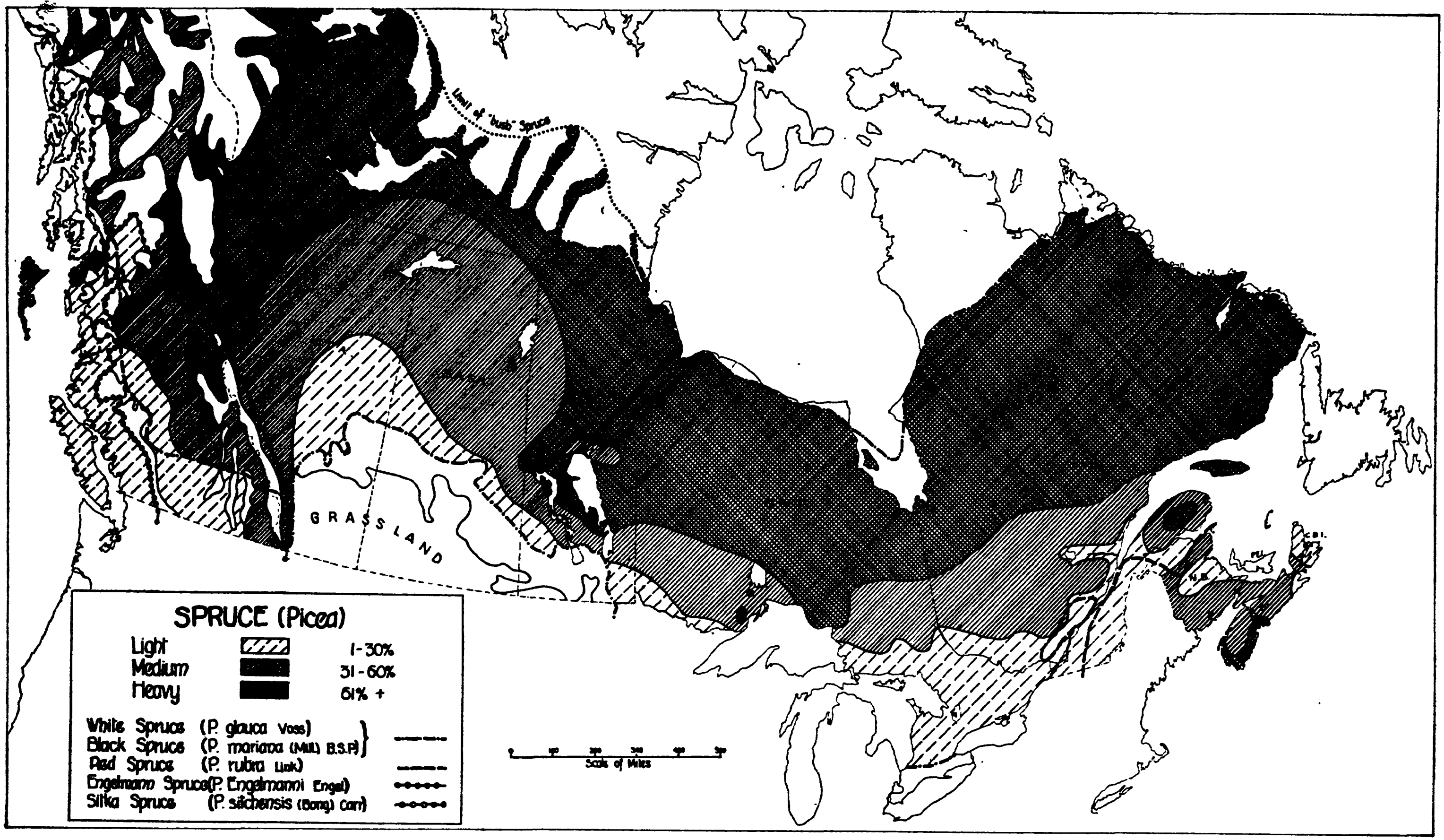
Limit of "bush" Spruce
GRASSLAND
N.B.
P.E.I.
SPRUCE (Picea)
Light ▨ 1-30%
Medium ▩ 31-60%
Heavy ■ 61% +
White Spruce (P. glauca Voss)
Black Spruce (P. mariana (Mill.) B.S.P.)
Red Spruce (P. rubra Link)
Engelmann Spruce (P. Engelmanni Engel)
Sitka Spruce (P. sitchensis (Bong.) Carr)
0
100
200
300
400
500
Scale of Miles

FIG. 2. Map of population intensity of spruce.

being especially striking in the White River area, immediately northeast of Lake Superior. In the Prairie Provinces, the belt of heavy spruce swings northward of this isotherm, a condition due no doubt to the numerical influence of poplar north of the Grassland formation. Heavy spruce also pushes southward from the Mackenzie region along the Rocky Mountains.

Over the southern portion of the boreal forest the population intensity of spruce is medium, comprising between 30 and 60 per cent of the total stand. The southern boundary of this belt in Eastern Canada shows a well-marked correlation with the southern boundary of the Boreal Forest (Halliday, '37).

South and west of this medium belt are areas where spruce stands are light (comprising less than 30 per cent of the total stand), principally situated in western British Columbia, north of the Prairies, and in the Ottawa and the St. Lawrence Valleys. In extreme southern Ontario, the southern limit of black spruce and white spruce corresponds to the boundary between the Carolinian and Alleghanian life-zones of Merriam ('98), the Carolinian and Canadian biotic provinces of Dice ('38), and between the Deciduous and Great Lakes forest regions of Halliday ('37). In British Columbia, the southern limit of these two species roughly coincides with the 51st parallel, as far west as the interior slope of the Coast mountains.

The map clearly indicates the present dominant position of white spruce and black spruce in the northern parts of the Dominion, and the extent to which these species have been able to spread over the former ice-covered area.

The two species in question are classed by Hultén as radiants from Northern Beringia which had reached the Mississippi drainage basin and the Atlantic Coast in the D-interglacial (Yarmouth) period. They were thus able to survive the maximal or Illinoian glaciation and the later but less extensive Wisconsin glaciation in many refugia south of the ice, as well as in the unglaciated Yukon Valley and perhaps along the exposed Atlantic continental shelf. The evidence of bog pollen shows early re-invasion of the species from the south; for all stations sampled, from Minnesota and northwestern Wisconsin eastward to the Atlantic Coast, show a marked preponderance of microfossil spruce pollen in the lowest horizons. White spruce, as well as black spruce, has also been found in late Pleistocene deposits at Minneapolis (Cooper and Foot, '32).

The two species may be classed as "plastic" from their evident ability to repopulate. This fact, together with the number of refugia, would presuppose many available biotypes and considerable potential variability. For white spruce, examination of material recently obtained across Canada certainly appears to indicate several geographical races. At least one variety is now taxonomically recognized (*P. glauca albertiana* R. Br. (*Abies arctica* Murray)), which is probably related to the Yukon refugium. There is reason to believe that this subspecies has spread eastward to meet with the more typical *P. glauca* in the Province of Manitoba (Dr. C. C. Heimburger; unpublished notes), and also southward down the lower slopes of the Rocky Mountains, on whose eastern slopes hybridization with Engelmann spruce is particularly evident.

Sitka spruce is considered by Hultén to be one of a group of western American coast radiants that probably survived maximum glaciation south of the ice boundary and subsequently spread northward along the coast towards Alaska. As the map shows, this species is confined to the shores of the Pacific Ocean.

The second western species, Engelmann spruce, is found between the Coast Range and the backbone of the Rocky Mountains, but does not reach farther north than the 57th parallel. Its present distribution indicates that it probably moved in from a southern center in postglacial times.

The remaining species, red spruce, derives from eastern American or Appalachian sources. Historically it belongs to that group of eastern conifers and broad-leaved trees differentiated out in Cenozoic times by the destruction of the land bridge between eastern America and Europe (see also: balsam fir, large-toothed aspen, wire (grey) birch and yellow birch). During glaciation it would have survived in refugia south of the ice on the Appalachians or perhaps on the continental shelf. Its present distribution has several interesting features: a comparatively limited advance into ice-freed country; evidence of correlation with high mean annual rainfall (figure 5); an island of colonization on the lower slopes of the Laurentian Hills (see Heimburger and Porsild, '38), which may have been separated from the main body by the Champlain Sea; and the presence of outliers as far west as Algonquin Park and Haliburton County, Ontario.

Pines

There are nine species of pine in Canada. Western white pine and ponderosa pine occur in southern British Columbia. Red and white pine extend across the southern part of Eastern Canada, and pitch pine (*Pinus rigida* Mill.) enters Canada only in the Thousand Islands region of eastern Ontario. Limber pine (*P. flexilis* James) and white-bark pine (*P. albicaulis* Engelm.) occur sparingly in the western mountains. These species have, however, not been considered in the present paper, for various reasons. Many of them have only a restricted distribution in Canada, and others, such as white and red pine, and the corresponding western species, have been extensively affected by cutting and other destructive agencies.

Jack and lodgepole pine, closely similar in form and habits, between them cover Canada from coast to coast. They meet along the eastern foothills of the Rocky Mountains, overlapping in the Peace River districts, but with a gap between them in the northwestern corner of Alberta (figure 4).

Although these pines are characteristic of and adapted to the driest sites, it is not in the great region of lowest annual rainfall north of the Prairies that they are at present most abundant, but on either side of it in the Rocky Mountain foothills and between Lakes Winnipeg and Superior.

The area of heavy jack pine, however, extends above the western prairies into eastern Alberta. There is also a secondary concentration in the Algoma region of Ontario, separated from the northwestern Ontario "pineries" by the spruce-balsam flats east of Lake Nipigon. An area of medium population intensity of jack pine occurs in the interior of northern Quebec (Central Laurentian section, B3, of Halliday). Since the northern boundary of medium jack pine concentration (over 20 per cent of the total stand) would not be determined by rainfall, which diminishes northwards, it is possible that it may be limited by temperature; west of Lake Nipigon this boundary does conform reasonably well with the July isotherm of 16° C.; however, east of that lake there is no apparent correlation (figure 3).

It is noteworthy that the greatest region of jack pine concentration, in Kenora and Rainy River, has been the scene of the heavy outbreak of the jack pine budworm which has appeared in the last decade.

Throughout the remainder of Eastern Canada, jack pine makes up less than 20 per cent of the total stand, being notably absent in certain sections. It does not approach to within a hundred miles of the northern boundary of the Prairies. Though present in Michigan, it is absent or scarce in southern Ontario, the St. Lawrence Valley, the Eastern Townships of Quebec, the Gaspé, the upper St. John Valley, and Nova Scotia. Moreover it stops short of the northern timber line by several hundred miles, the limit of its range to the north roughly approximating

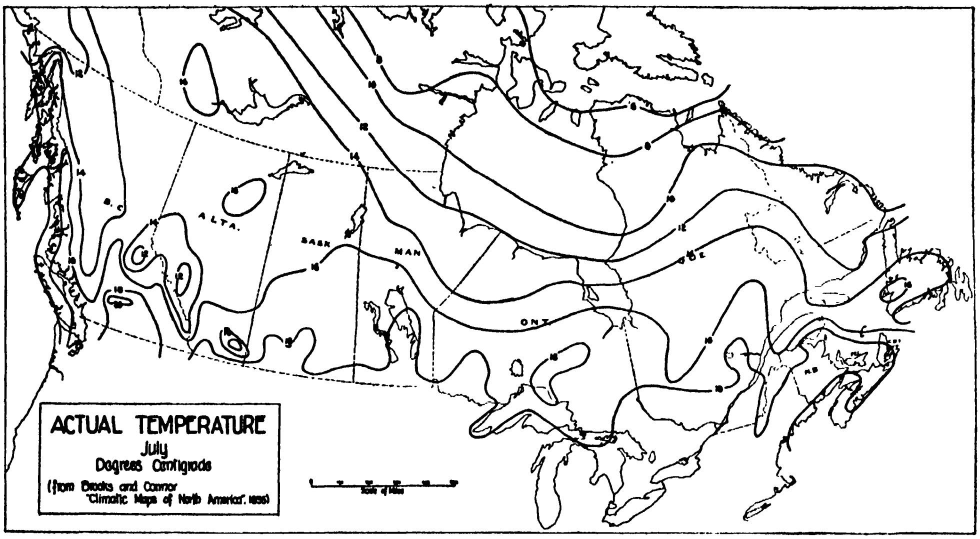

FIG. 3. July isotherms of actual temperature in Canada.

the 14° C. July isotherm west of Hudson Bay. To the east, however, on the highlands of northern Quebec factors other than temperature evidently limit its present range.

It has been stated by Fernald ('19) that the distributional peculiarities of jack pine are related to the distribution of acid soils of granitic origin, that is, that the species is a "pronounced oxylophyte." It must be noted, however, that individual jack pine reaches its maximum size on the neutral or basic soils of the Cretaceous escarpment in Western Canada. Moreover, it is found on the limestones of the interlakes area of Manitoba, and of Bruce Peninsula and western Manitoulin Island.

Lodgepole pine occurs in its heaviest stands in the rain-shadow of the Coast Mountains and Rocky Mountains, i.e., in the cool dry northern interior of British Columbia, and the high foothills of western Alberta. Elsewhere, on the Pacific Coast, in the interior dry and wet belts of British Columbia, and in Yukon Territory, it is found sparingly (less than 20 per cent of the total stand). The eastern boundary of lodgepole pine does not extend farther than 200 miles east of the Rockies, though "islands" of it occur on the Cypress Hills of southeastern Alberta, and on the middle Hay and lower Peace Rivers.

The accompanying map (figure 4) may be profitably examined in the light of the theory of refugia. There is a strong indication that the main repopulation of jack pine took place from a region southwest of the Great Lakes and has spread out in a two-fingered fashion east and west. Correlation is suggested in part with the "driftless area" of Wisconsin. The existence of an important Wisconsin refugium is corroborated by the peat bog studies of Wilson ('38), who considers jack pine (with spruce) to have formed the first forests on the lighter sandy soils of the northwest portion of that State. The separate occurrence of this species in the Maritimes may be connected with a continental shelf refugium, unless it is considered that jack pine is a receding species in southeastern Canada.

Lodgepole pine is classed by Hultén among a group of continental western American radiants that had reached south of the 40th parallel before devastation by maximal glaciation. By Wisconsin times, a more or less continuous area had been re-established, which was doubtless only

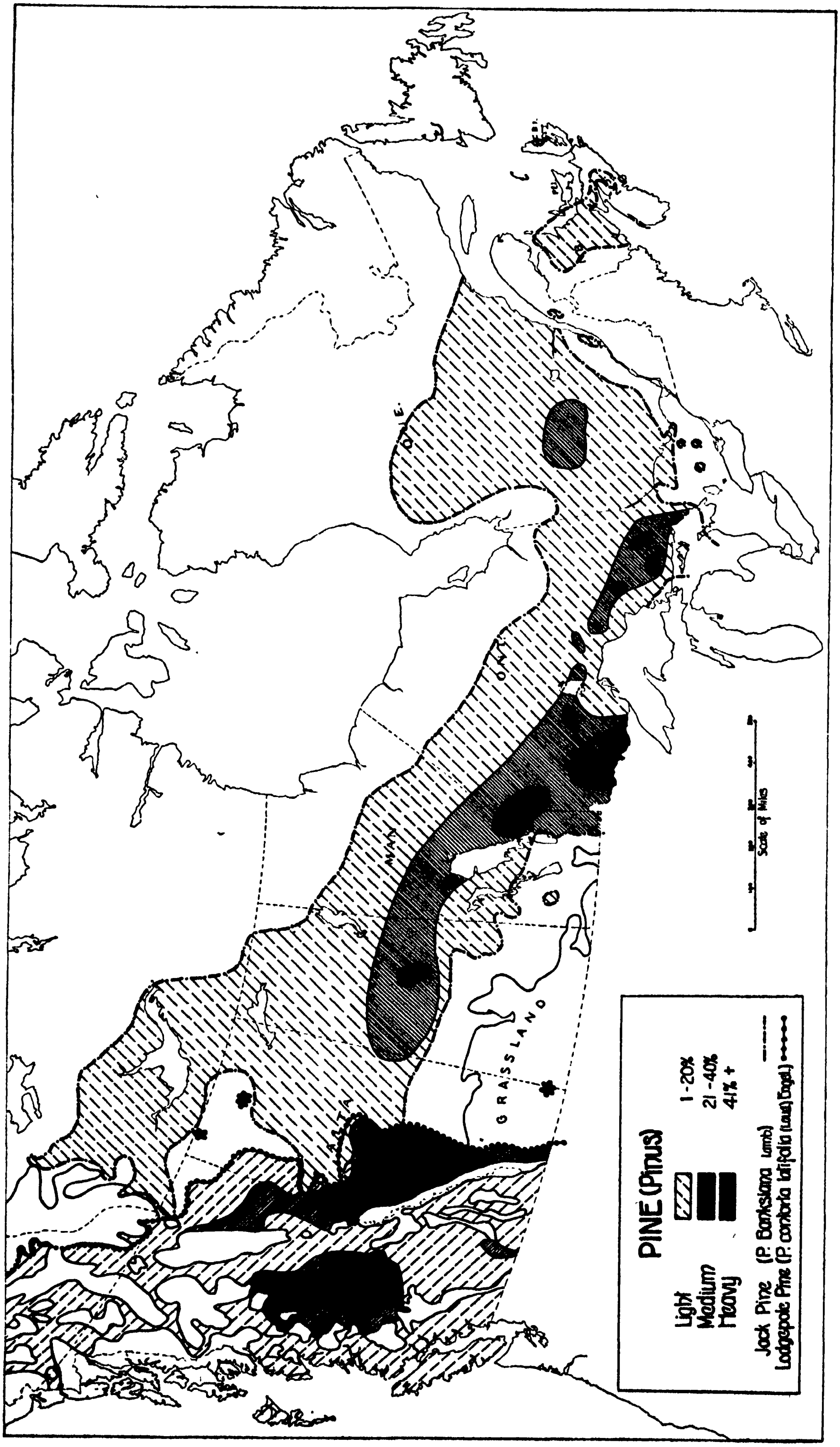

FIG. 4. Map of population intensity of jack pine and lodgepole pine.

split up into a number of elementary areas (minor refugia) by the Cordilleran ice-sheets, which refugia in turn were readily able to fuse together again. The heavy concentration shown on the map as centering on the east side of the Coast Mountains may relate to this condition, further corroboration being afforded by the map for alpine fir, another member of the group. A similar concentration along the foothills of the Rocky Mountains is intriguing in view of the possible existence of an ice-free corridor in Alberta between the Keewatin and Cordilleran ice-sheets. In this connection, it is significant that Raup ('35) found lodgepole pine on the apparently unglaciated higher elevations of the Caribou Mountains, and that the species also occurs on the Cypress Hills of southeastern Alberta.

FIR

Four species of fir are found in Canada. Balsam fir covers Eastern Canada, with a tongue extending over the northern boundary of the prairies to reach northern Alberta. Alpine fir is distributed throughout Yukon Territory and British Columbia, except in the middle Fraser Valley, sending a tongue northwestward into northern Alberta. Amabilis fir in Canada is confined to the Pacific Coast, while grand fir extends north from the western United States into Vancouver Island and the adjacent mainland, and the upper Kootenay Valley (figure 6).

Heavy stands of balsam fir (comprising 30 per cent of the total stand) are confined to both shores of the lower St. Lawrence River—the Cote Nord, Anticosti Island, and the Gaspé—and to Cape Breton Island and Guysborough County, Nova Scotia. In certain parts of Gaspé and Cape Breton Island balsam fir is in excess of 50 per cent of the total stand.

Medium population intensities (comprising 11 to 30 per cent of the total stand) of balsam fir surround these areas. From examination of the rainfall map it will be seen that the northwestern boundary of this category shows good correlation with the isohyet of 30 inches mean annual rainfall (fig. 5). An additional but smaller area of medium population intensity is found to the northeast of Lake Superior, extending from Algoma to Lake Abitibi. Separation of the two areas by a corridor of light population intensity may be associated not only with the extension of mixed forest up the Ottawa River, but also with the extensive destruction of balsam fir by the outbreak of spruce budworm around the year 1920,

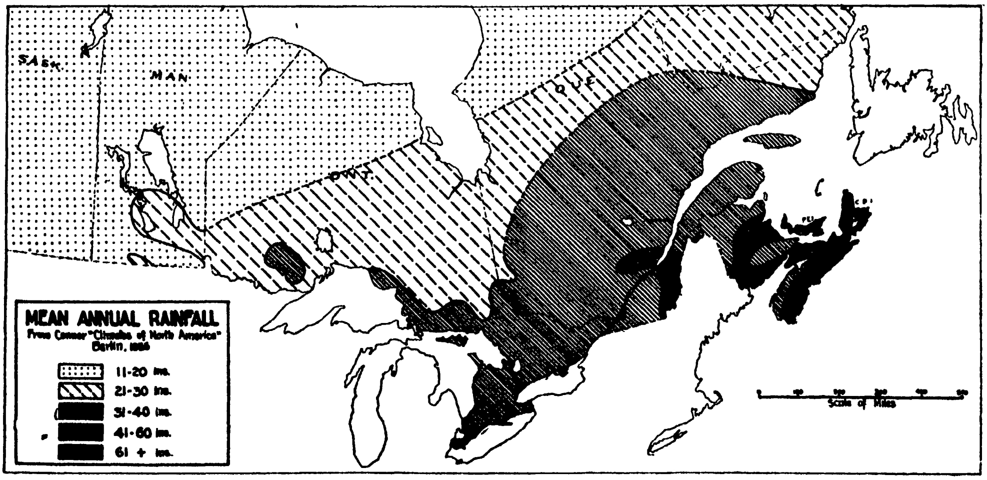

FIG. 5. Map showing mean annual rainfall in Eastern Canada.

just before the survey data employed were obtained.

The area of medium population intensity is subject to periodical attacks of spruce budworm, which serve to reduce the volume of balsam fir for a period, but after some thirty years this species recovers in volume by reason of its abundant regeneration in the infested areas. Serious outbreaks of hemlock looper (in the lower St. Lawrence Valley) and of black-headed budworm (in Cape Breton Island) are restricted to the area of heavy concentration of balsam fir.

Throughout the center of the continent, from Lake Superior and James Bay to the Athabaska River, balsam fir is of only light population intensity (comprising less than 10 per cent of the total stand). This is a region of low rainfall, from 25 down to 10 inches annually. Dry sites and repeated forest fires militate against the growth of balsam fir. Proceeding westward in this area, stands of balsam fir become increasingly scattered and more and more restricted to compensating habitats, such as valleys and north-facing slopes. The effect of dry climate on the growth of fir (in this case alpine fir) may be noted also in the interior of British Columbia and Yukon. On the windward slopes of the Coast, Selkirk, and Rocky Mountains, fir again becomes abundant. In fact, the map of the abundance of fir throughout Canada will be found to resemble quite closely the map of mean annual rainfall (figure 5).

The map of population intensity very strongly suggests the existence of major refugia for balsam fir during Wisconsin times along the exposed eastern continental shelf, and in Newfoundland, as well as south of the ice front. This species, although now ranging well into the boreal forest, also extends down the backbone of the Appalachians, and a closely-related endemic species, *A. fraseri* (Pursh.) Poir., is found in the southern part of these mountains. Bog pollen studies show balsam fir to have been one of the first forest invaders of the ice-freed areas as far west as Minnesota, and remains of a tree belonging to the genus *Abies,* attributed to the late E-interglacial just previous to the Wisconsin period, were found in Pleistocene deposits near Toronto (Penhallow, '07).

Alpine fir has been listed by Hultén among his continental western American radiants, a group which is presumed to have survived the Wisconsin glaciation as small elementary areas in the northern Rocky Mountains, as well as in unglaciated Yukon and south of the ice. The heavy percentage shown by the map for the Babine-Stikine region of British Columbia is significant in this respect.

Amabilis fir is a western American coast radiant that for the most part evidently survived south of the ice during the Wisconsin glaciation and re-invaded northwards. Local ice-free coastal slopes between glaciers may have been factors in providing nuclei for re-invasion, and the high proportion of this species on the mainland east of the Queen Charlotte Islands may be indicative in this respect.

The remaining species, grand fir, obviously derives from a center well south of the ice-front. Re-invasion along the coast was paralleled by a movement up the Kootenay Valley to the southern part of the interior wet belt.

WESTERN HEMLOCK

The heaviest stands of western hemlock, amounting to over 30 per cent of the total forest composition over considerable areas, are to be found on cool moist sites on the Queen Charlotte Islands, northern Vancouver Island, and throughout the Skeena region. Its population intensity falls below 15 per cent on the leeward side of the Coast Mountains and those of Vancouver Island. Its distribution stops short of the interior dry belt of British Columbia, to reappear on the rainy westward slopes of the Rocky Mountains almost as far north as Prince George. It again attains medium population intensity (over 15 per cent of the

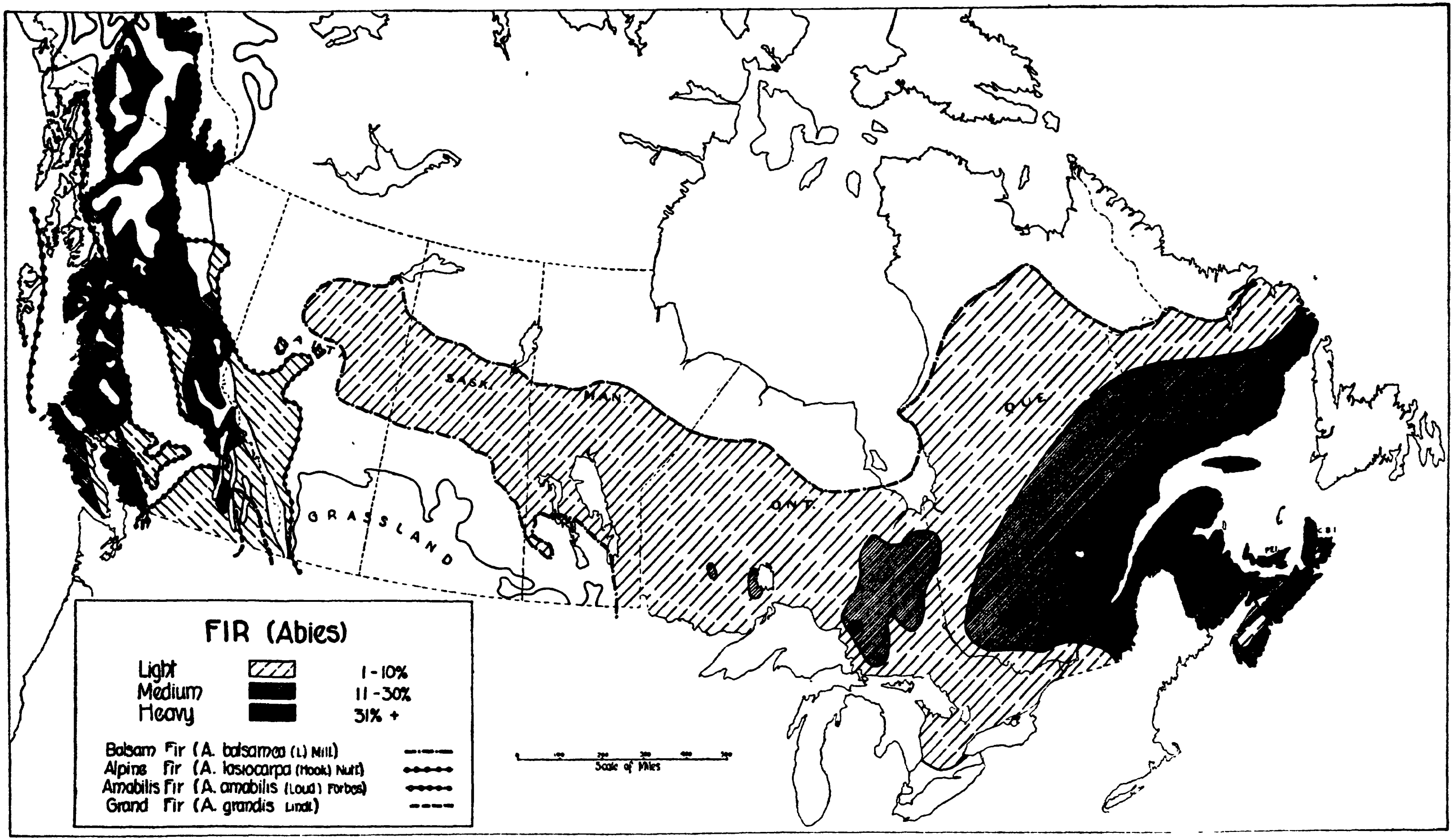
FIR (Abies)
Light ▨ 1-10%
Medium ■ 11-30%
Heavy ■ 31% +
Balsam Fir (A. balsamea (L) Mill)
Alpine Fir (A. lasiocarpa (Hook) Nutt)
Amabilis Fir (A. amabilis (Loud) Forbes)
Grand Fir (A. grandis Lindl)
0
Scale of Miles
GRASSLAND
SASK.
MAN.
ONT.
QUE.
P.E.I.
C.B.I.
ALTA.

FIG. 6. Map of population intensity of fir.

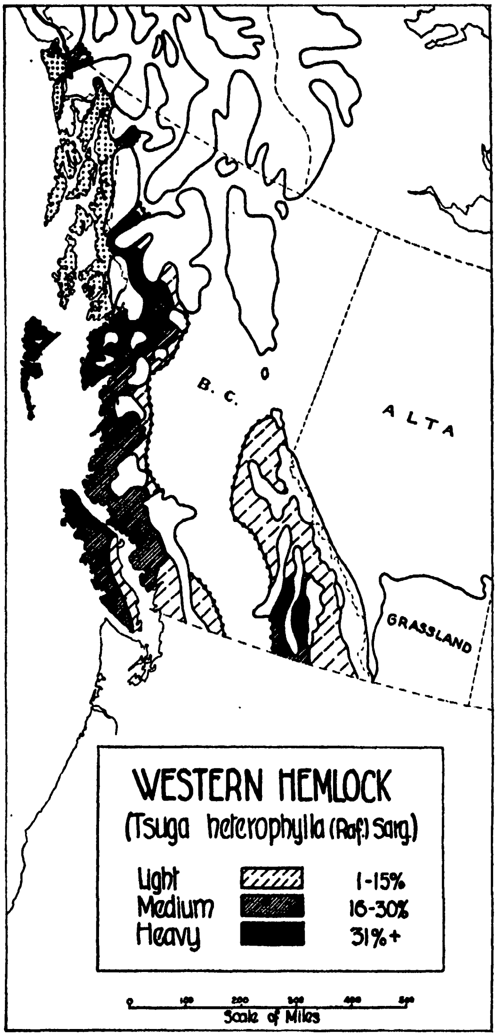

FIG. 7. Map of population intensity of western hemlock.

total stand) in the Kootenay region on the westward slopes of the Selkirk Mountains (figure 7).

Along the Pacific Coast western hemlock extends northward well into Alaska. Mountain hemlock (*T. Mertensiana* (Bong.) Sarg.) occurs in the Coast Mountains, extending north to the same latitude.

Western hemlock, like Sitka spruce and amabilis fir, is one of Hultén's western American coast radiants, spreading originally from southern Beringia in the D-interglacial period, but ranging further inland than the above trees. Large areas were evidently available for its survival south of the Cordilleran ice-sheets, and it has repopulated as far north as the Kenai Peninsula, and has also reached the upper tributaries of the Columbia River system. The possible existence of more northern, isolated, refugia is suggested by the present heavy concentration around the Skeena Valley and in the Babine-Stikine region. A similar situation is found in the Queen Charlotte Islands, the northern portion of which, according to Hultén, contains unglaciated areas.

DOUGLAS FIR

The pattern of population intensity for Douglas fir (figure 8) is the reverse of that for western hemlock. The areas of maximum population intensity, where it comprises more than 50 per cent of the total stand, are located on the east side of Vancouver Island, in the great Interior Dry Belt, and in the Kootenay Valley in the lee of the Selkirk Mountains. It is actually absent from the Queen Charlotte Islands, the north end of Vancouver Island, and the valley of the Skeena River. Its northern limit is near the Finlay Forks on the 56th parallel.

Douglas fir attains its greatest size in the southeastern part of Vancouver Island. Its heaviest population intensity is attained in the middle Fraser Valley, reaching over 90 per cent of the total stand in the region between Lillooet and Williams Lake. Within its range, this species shows marked differences in size and form, broadly related to the climatic conditions under which it grows. This has led to the recognition of at least two forms, one associated with the Pacific Coast, the other with the drier interior.

As a Cordilleran species of wide range, only the more northern stands would have been affected by glaciation. The present distribution pattern in the United States strongly suggests that re-invasion took place from two centers, one approach being along the coast and possibly up the Columbia Valley, the other from a Rocky Mountain or continental source which may have repopulated the interior plateau of British Columbia. The local distribution in Canada east of the Rocky Mountains also derives from the latter source and appears to have come directly from the south rather than from the west. The two forms mentioned earlier may well relate to these two main centers of dispersion.

POPLAR

A number of species of poplar are found in Canada. Trembling aspen is by far the most abundant species, extending from the Atlantic to the Pacific, and north almost to the tree limit, with its northern boundary roughly approximating the July isotherm of 13° C. (figure 3). Balsam poplar (*Populus tacamahacca* Mill.) also extends across the continent from Newfoundland to Alaska, but is absent from the greater portion of British Columbia. Large-toothed aspen is found in Eastern Canada south of the 50th parallel and extending west to Lake of the Woods. Black cottonwood (*P. trichocarpa* Torr. and Gray) is found throughout British Columbia and the Yukon, west of the Rocky Mountain divide. Other species of cottonwood (*P. deltoides* Marsh., etc.) are to be found in the southwestern part of the Prairies, and at scattered points in southern Ontario and Quebec.

The greatest concentration of poplar is to be found in the region north of the Prairies (figure 9). There it comprises over 90 per cent of the total stand in the Aspen Grove belt (Halliday, '37) bordering the Prairies, while population intensities of over 30 per cent extend east to Lake of the Woods, and north to Lake Athabaska. The map makes it clear that poplar is typical of the three Prairie Provinces. The effect of cutting and forest fires has been, however, to increase considerably its numerical proportion in certain parts of Eastern Canada, namely the Ottawa Valley, Nipissing and eastern Algoma, parts of the Northern Clay Belt, and the middle St. John Valley. It is in these areas that the extensive outbreaks of forest tent caterpillar have occurred during the past half-century.

Throughout the remainder of the forest regions in Eastern Canada, especially where undisturbed by man, poplar is comparatively scarce (comprising less than 10 per cent of the total stand). In British Columbia it is also of generally light abundance, with the exception of certain areas in the north of the province.

Balsam poplar and trembling aspen are definitely plastic species and have been

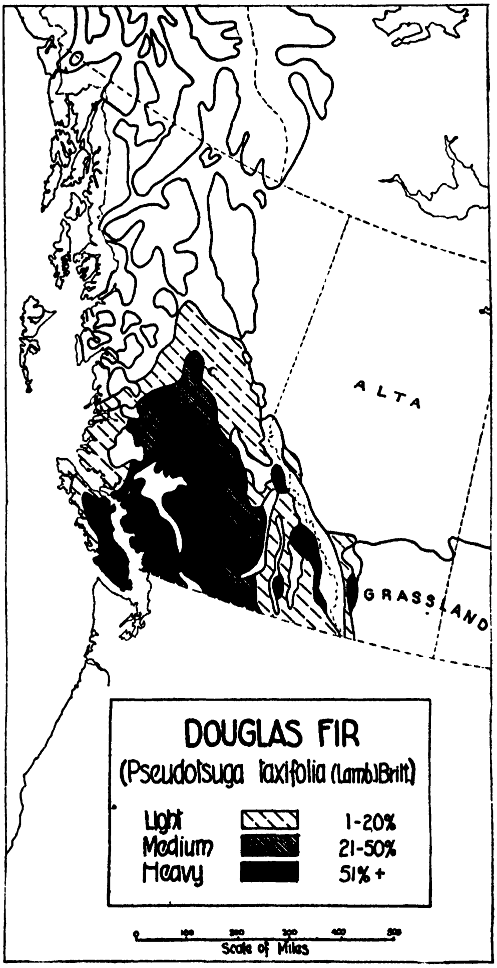

FIG. 8. Map of population intensity of Douglas fir.

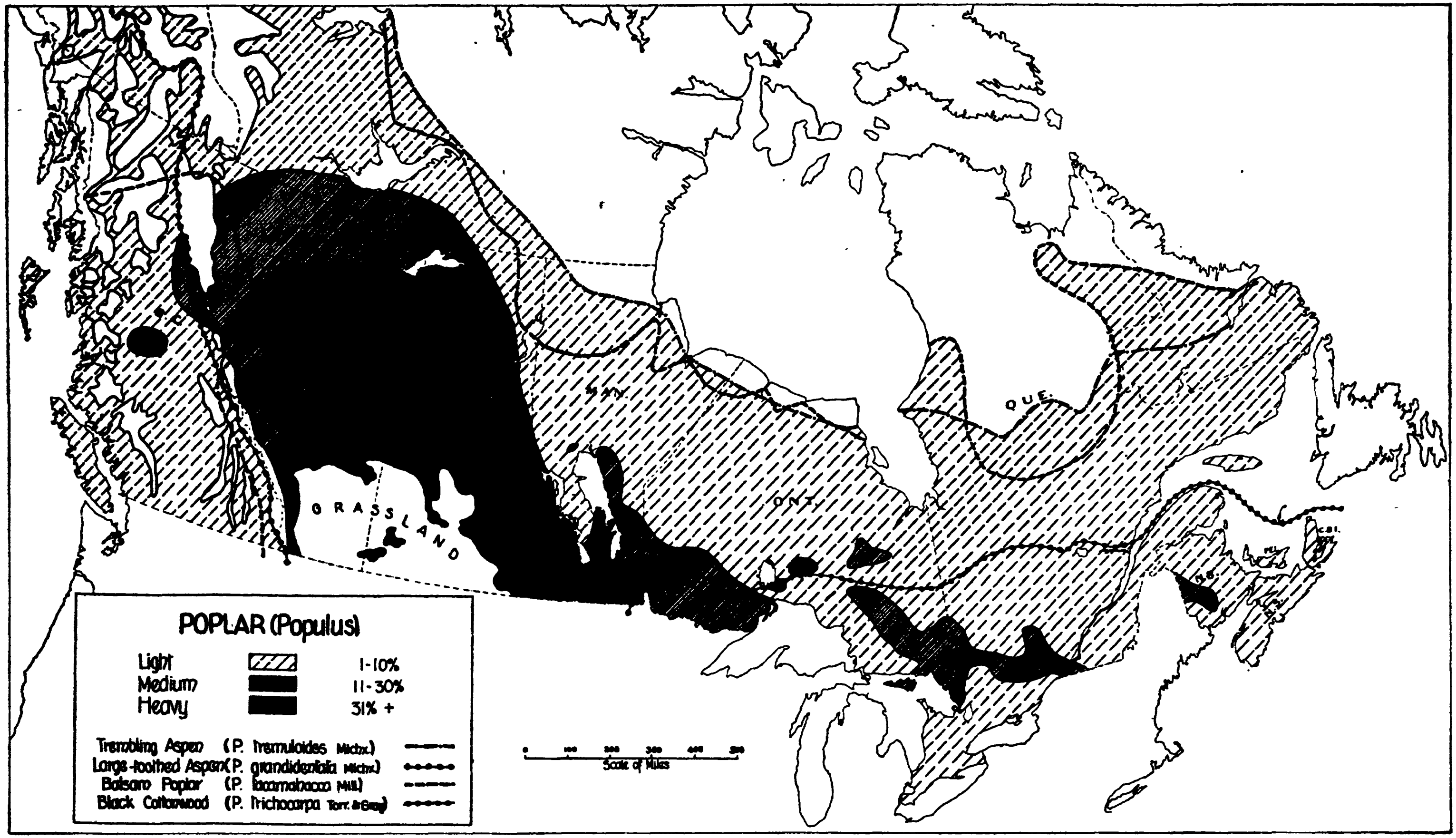
POPLAR (Populus)
Light 1-10%
Medium 11-30%
Heavy 31% +
Trembling Aspen (P. tremuloides Michx.)
Large-toothed Aspen (P. grandidentata Michx.)
Balsam Poplar (P. tacamahacca Mill.)
Black Cottonwood (P. trichocarpa Torr. & Gray)
Scale of Miles
0
100
200
300
400
500
B.C.
GRASSLAND
MAN.
ONT.
QUE.
N.B.
C.B.I.

FIG. 9. Map of population intensity of poplar.

able to recolonize almost the whole of the ice-freed area. Not only are they provided with abundant and very light windborne seed, but also they can dominate rapidly after disturbances such as fire, through abundant production of rootsuckers. As light-demanders, however, their principal parts are played in early successional stages.

Hultén places trembling aspen and balsam poplar among his western American continental radiants, as boreal American plants that had reached from coast to coast before maximum glaciation. They evidently survived glacial conditions on numerous refugia south and east of the ice-sheet, as well as in the Yukon Valley, whence they have been able to regain their original range.

The heavy concentration, of aspen particularly, around the Grassland formation is in part a function of adaptability to climate and lack of competition, but may also bear a relation to repopulation centers southwest of the Great Lakes. The extension of abundance northward through the centers of Saskatchewan and Alberta may be connected with the apparent immaturity, post-glacially, of much of the vegetation cover there (Raup, '35). Fire, in particular the far-reaching conflagrations of the decade 1885–1895, has also been a marked factor (Moss, '32). On the other hand, there is evidence to indicate that trembling aspen has noticeably extended its range southwards into the Grassland in the last half-century, probably because of elimination of prairie fires through cultivation.

The large-toothed aspen is one of several eastern American species characteristic of the Great Lakes, the St. Lawrence River, and the northeastern Atlantic seaboard. It was probably able to survive glaciation in the southern part of its present range.

Black cottonwood, a Cordilleran species of wide north and south distribution, is considered by Hultén as a continental western American radiant. Only a part of its range would have been affected by maximal glaciation, and in postglacial times it was able to recolonize from many refugia. The present distribution, especially in the interior, is largely confined to the river valleys.

WHITE BIRCH

White birch extends across the continent from the Atlantic Coast to the Rocky Mountains, and northward to the 13° C. July isotherm, with outlying pockets extending almost to the absolute tree limit. In the west, the distribution and taxonomic relationships of this species complex are not yet clear. However, a western variety (*B. papyrifera occidentalis* Sarg.) has been recognized in the lower Fraser Valley, and a second variety (*B. papyrifera neoalaskana* (Sarg.) Raup) has been described as extending from Lake Athabaska northwestward. Grey or wire birch (*B. populifolia* Marsh.), a closely-related species, is found in abundance in the Maritime Provinces and in the St. Lawrence Valley below Lake Ontario.

The general population intensity of white birch (figure 10) is quite similar to that of balsam fir, and shows a corresponding correlation with total rainfall, with the exception that white birch becomes relatively scarce on the shores of the Gulf of St. Lawrence. The region of greatest concentration is to be found on the highlands at the headwaters of the Ottawa River in western Quebec. Smaller foci of population intensity occur on the upper Mississagi River in Algoma, the upper St. John River in New Brunswick and immediately west of Lake Nipigon. Westward from Lake Superior, the population intensity of birch decreases to less than 10 per cent, while in the Prairie Provinces it rarely exceeds 2 per cent.

Another plastic species, the white birch has re-occupied a large extent of the land originally ice-covered. Classed by Hultén along with trembling aspen and balsam poplar as a western radiant of continental character, it is generally a much more

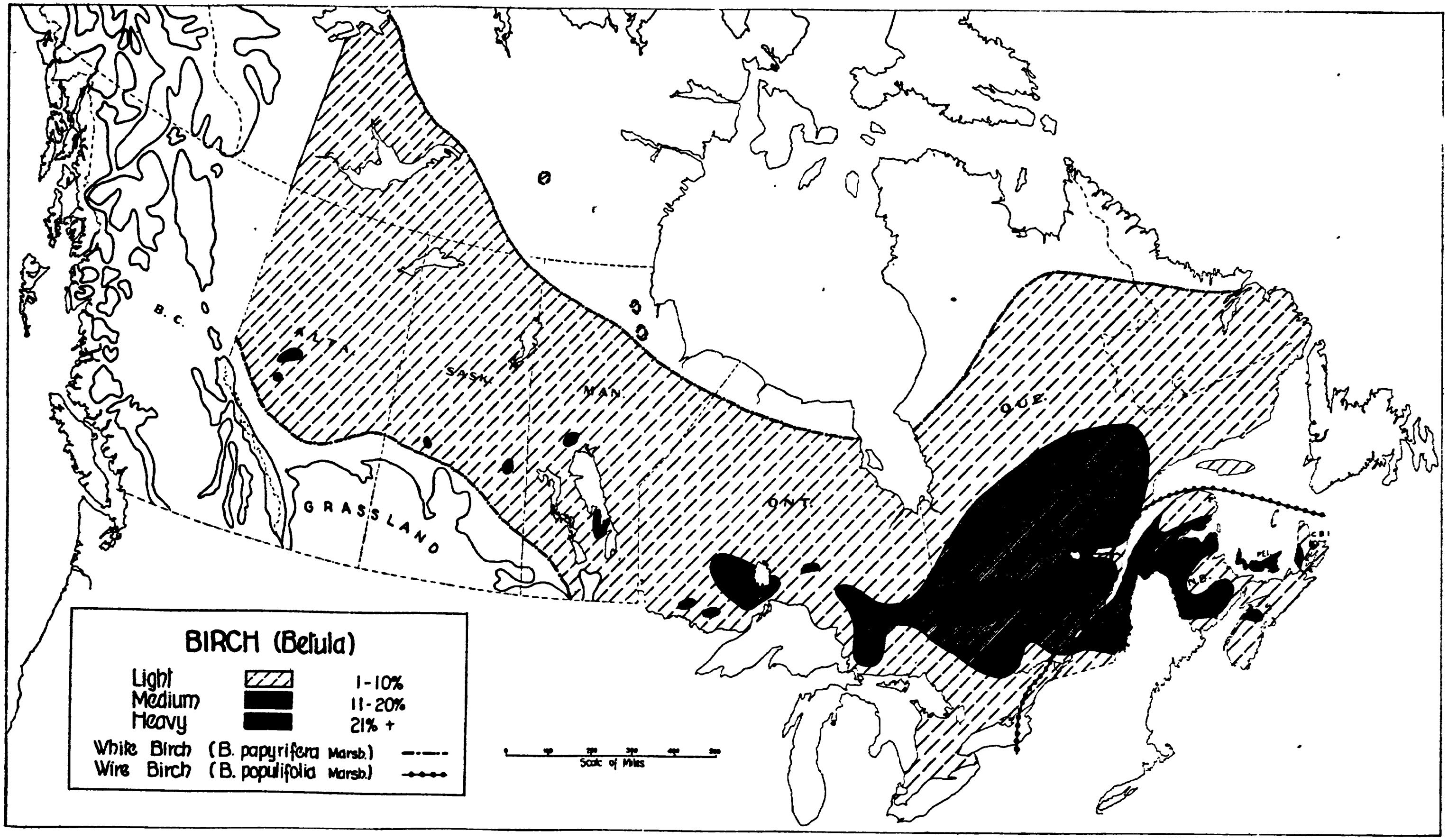

FIG. 10. Map of population intensity of white birch and wire birch.

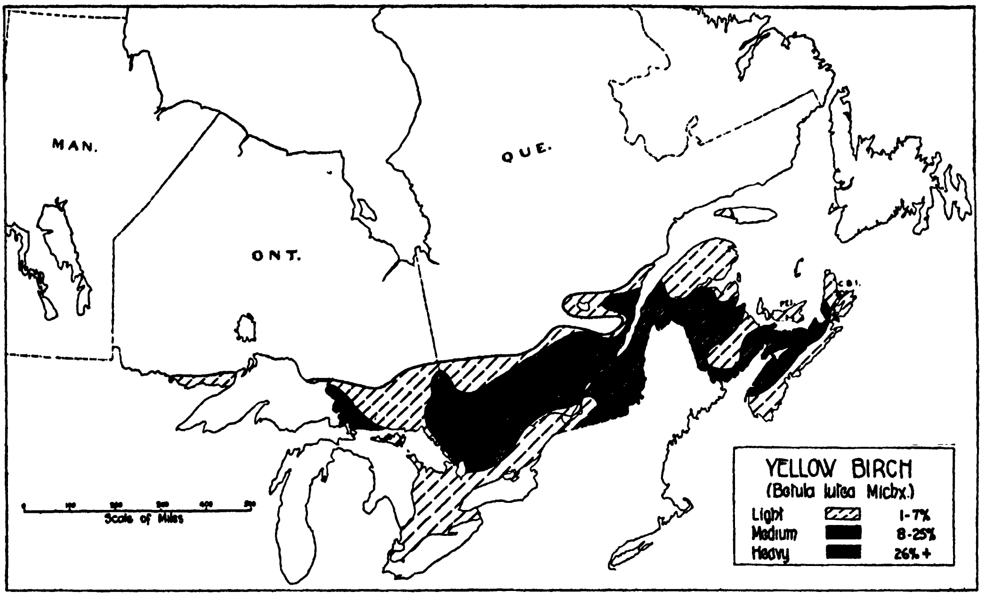

Fig. 11. Map of population intensity of yellow birch.

scattered species and is not found in the near vicinity of the Grassland.

The map would suggest a well-marked refugium either on the eastern continental shelf or along the Appalachians. In the center of the continent, Cooper and Foot ('32) found this species in late-Pleistocene deposits at Minneapolis, suggesting the Wisconsin-Iowa refugium. The two varieties of the species mentioned above may well relate respectively to refugia south of the Cordilleran ice and in the Yukon Valley, radiants from the latter area having now reached at least north central Alberta.

The range of wire birch closely resembles that of red spruce, and their history and behavior during glaciation have, no doubt, been similar. It was able to survive the Wisconsin period on refugia south of the ice along the Appalachians and possibly on the exposed continental shelf. In this connection it is interesting to note that, according to the compilation of Munns ('38), a solitary outlier occurs on the east side of Newfoundland, on an area that was covered by the local ice-sheet of that island, but no great distance from portions to the south and west stated to have been ice-free during the last glaciation (figure 1).

Yellow Birch

Yellow birch is restricted to Eastern Canada, being most abundant in the areas surrounding the lower Great Lakes where the mean annual rainfall exceeds 30 inches. Its northern limit very largely determines the boundary of the Great Lakes St. Lawrence Forest Region, within which it is most abundant on cool moist highlands (figure 11).

Areas of greatest concentration, where it forms over 25 per cent of the total stand and is the most abundant single species, are the southeast coast of Lake Superior, the southwestern half of Algonquin Park, the middle Gatineau-Lievre and the St. Maurice drainage systems, the highlands west of Magantic in southern Quebec, the upper St. John Valley, and the shores of the Bay of Fundy. The region of medium population intensity, where yellow birch makes up more than 8 per cent of the total stand, extends in a belt from Northumberland Strait and the Lower Saguenay River west to Georgian Bay, with an outlying area in southwestern Algoma.

This "northern hardwood" is a member of a well-defined group of trees characteristic of forest regions centering on the Great Lakes and the northern Appalachians, and extending to the Atlantic and Newfoundland (Nichols, '35; Halliday, '37) and which, previous to maximal glaciation, probably occupied much the same territory as to-day.

During the Wisconsin glaciation it is probable that refugia for the species were available on the eastern continental shelf, the Appalachian Mountains, and in Wisconsin. This is strongly suggested by the present areas of high population intensity, which also indicate the influence of land bridges across the Great Lakes system (e.g., Sault Ste. Marie) and of the Mohawk and Champlain Valleys as re-invasion channels.

SUMMARY

1. This paper presents a series of maps to show the geographical distribution of certain tree species in Canada, not only by the boundaries of their range, but also by contours showing their population intensity within this range.

2. This was accomplished by plotting the relative percentage by volume of a given species to the total forest composition in a great number of unit areas surveyed, comprising at least 85 per cent of the area of merchantable timber in Canada.

3. While certain disadvantages in this method are pointed out, it is considered that it affords as accurate a picture as can be derived from the data available and thus may form a valuable complement to a forest classification of Canada.

4. With due caution, certain inferences are drawn with regard to the relationship of these tree species to present climate, and the possible course followed in their repopulation of the Canadian land-mass following Wisconsin glaciation.

5. The tree species treated in the maps are red, black, white, Engelmann and Sitka spruce, jack and lodgepole pine, balsam, alpine, amabilis and grand fir, Western hemlock, Douglas fir, trembling and large-toothed aspen, balsam poplar, black cottonwood, and white, wire and yellow birch.

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CORRELATION OF THE HABITATS OF AMPHIBIANS WITH THEIR ABILITY TO SURVIVE THE LOSS OF BODY WATER[1]

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INTRODUCTION

Even the most casual observer has noticed that the various species of amphibians do not frequent the same type of surroundings. A student of ecology finds that practically every species of amphibian has a distinctive habitat, and that the habitats range from strictly aquatic to almost totally terrestrial.

In the transition from the aquatic to the terrestrial mode of life among amphibians, the problem of the conservation of body moisture presents itself. To an aquatic species which is constantly bathed in water, this offers no difficulty. But a terrestrial species is obviously exposed to the effects of evaporation for long periods of time, and therefore must replace the surface moisture lost through evaporation from its reserve within the body. In order to endure a comparatively dry habitat and to cope with the inevitable loss of body water, a terrestrial amphibian evidently must possess some adaptation not present in an aquatic form, or present in a smaller degree.

To explore this problem, a series of experiments were performed, in which, under controlled conditions, specimens of several species of amphibians were artificially subjected to drying conditions experienced in milder form in nature.

This paper presents (1) data based upon the careful measurement of the water lost through evaporation, (2) a comparison of the limits beyond which individuals of the species studied could not survive exsiccation, (3) a correlation of the vital limits of water loss with the habitats of amphibians, and (4) an explanation of one of the phases of the problem of the transition from the aquatic to the terrestrial mode of life among amphibians, i.e., that phase dealing with the loss of body water through evaporation.

APPARATUS

The apparatus used was essentially that described by Hall ('22), who determined the vital limits of water loss for a number of animals belonging to various phyla and orders, including 2 species of amphibians, *Rana pipiens* and *Ambystoma punctatum*. The purpose of the apparatus was to provide a steady flow of pure, dry air through a chamber where the specimens were exposed to the effects of evaporation. The air was bubbled through a series of 3 large bottles supplied with concentrated sulfuric acid to remove the atmospheric moisture. To neutralize any possible acid fumes, a small bottle containing sodium hydroxide pellets was placed next in the series. Glass wool in another small bottle removed any solid particles that might be present. A few lumps of litmus checked on the neutrality of the air, which was now ready for use, and was passed into the exsiccating chamber. This consisted of a large Whitall, Tatum museum jar equipped with a clamped-on lid. Through the glass lid 3 holes were bored, one for the air inlet tube, one for the outlet tube, and the third for a thermometer. These were carefully sealed in with sealing wax. A rubber gasket well covered with petroleum jelly was used to seal the jar when in use. The various containers were connected with glass and rubber tubing.

Air for the experiments was obtained

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[1] For time, suggestions, and courtesies extended, the authors are deeply indebted to Prof. Thevor Kincaid, Dr. George B. Rigg, Dr. Arthur Martin, Dr. Kenneth Kobe, Prof. W. L. Beuschlein, and Dr. J. M. Dille, all of the University of Washington faculty.

from the compressed air supply in the laboratory. It was found that the pressure of this system varied periodically with that of the compression tank. In order to insure a steady flow of air, a pressure release was inserted between the air supply and the first acid bottle. This apparatus consisted of a column of mercury in an eight-inch test tube supplied with a two-hole stopper. A long T-tube extended through the stopper to the bottom of the mercury. The air passed through the top of the T-tube, but if the pressure arose to a point higher than desired, it was reduced by the passage of air through the stem of the T, into the mercury, and out by way of a thistle tube inserted in the second hole of the stopper. The exact flow of air desired could be maintained by carefully adjusting the height of the mercury column. A trap was placed between the mercury column and sulfuric acid to prevent the reverse flow of acid into the mercury when the air supply was turned off.

To provide a constant check on the rate of flow, a manometer was placed just after the exsiccating chamber. This consisted of a large U-tube with the tops of the columns connected with a cross tube. In the middle of the cross tube was a constriction. When air was passed through this tube, the constriction caused increased pressure on the left side of the water column, forcing the right hand column to rise. A scale calibrated by means of a Sargent wet test meter was placed behind this column. The pressure release was adjusted to permit a flow of 2000 cubic centimeters of air per minute. Evaporation of the water column necessitated the checking of the water level and replacement of water when needed.

MATERIAL

Ten species of frogs and toads were used for the experiments. Five of these were species indigenous to southeastern United States and were purchased from a biological supply house in Florida. These included *Scaphiopus holbrookii* (Holbrook's spadefoot toad), *Bufo terrestris* (southern toad), *Hyla cinerea* (green tree frog), *Rana grylio* (southern bullfrog), and *R. sphenocephala* (southern leopard frog). One species, *R. pipiens* (common leopard frog), was obtained from another biological supply house in the East, while the following four species were collected in the state of Washington: *Scaphiopus hammondii* (western spadefoot toad), from Vantage, near the Columbia River; *Bufo boreas* (northwestern toad) from various points about Puget Sound; *Hyla regilla* (Pacific tree frog) from Chase Lake and near Anacortes; and *Rana aurora* (western wood frog) from the swamp on the University of Washington Campus.

PLAN OF PROCEDURE

An experiment proceeded as follows: The specimen was washed to remove any foreign particles adhering to the skin and immediately dried by the use of absorbent paper. After being carefully weighed, the specimen was placed at once in the exsiccating chamber. Only one specimen was exsiccated at a time. The lid was carefully clamped in place and was not removed until the end of the experiment. The time was noted as the air flow was turned on. Temperature and air flow were checked periodically and adjustments made if needed. The condition of the body, state of activity, and other observations were noted and the time was again recorded when the frog or toad was removed. After the exsiccated specimen was weighed, it was placed in a container where it was surrounded by water-soaked paper towels to allow it an opportunity to regain the water lost. In most instances the amount of water lost was fully replaced in from 12 to 24 hours. The specimens were marked by clipping the webs of the hind feet, and a record was kept of the survival or death of each individual.

Since this study consists essentially of comparative measurements, it was considered of the utmost importance to maintain as similar conditions as possible throughout the series of experiments, both for species and for individuals.

Great care was taken to maintain an equal flow of air for all experiments. Kunde ('57) and Durig ('01) stated that frogs died after a loss of nearly 15 per cent of their weight if the evaporation was rapid, whereas more than twice that loss could be survived if it was slow. Noble ('31) also made the statement that the rapid drying of amphibians was far more deleterious than slow drying. The manometer and mercury column were therefore checked frequently to assure a steady flow of 2000 cubic centimeters of air per minute.

It was essential that the temperature be maintained as constant as possible, for Holmes ('32) stated that amphibian respiration took place much more rapidly when the temperature was increased. Shelford ('13) reported that a rise of approximately 15 degrees Centigrade doubled the evaporating power of air by lowering the relative humidity. Thus a difference of 5 or 6 degrees, which is common in most laboratories, might seriously effect experimental results. In these experiments a constant temperature of 21

TABLE I. *Exsiccation data*

	1 Orig. Wt.	2 Dry Wt.	3 Loss	4 Pct. Loss	5 Time	6 Survived	7 Condition when removed
				Scaphiopus holbrookii			
1.	12.94	7.09	5.85	45.2	26:10	Yes	Extremely sluggish; dry.
2.	14.55	7.55	7.00	48.1	24:50	Yes	No activity; stiff; dry.
3.	16.20	8.40	7.80	48.1	26:40	Yes	Entirely inactive; dry.
4.	8.54	4.23	4.31	50.4	14:50	No	Slight movement; stiff and dry.
				Scaphiopus hammondii			
1.	15.49	8.21	7.28	46.9	21:30	Yes	Stiff; inactive.
2.	14.67	7.73	6.94	47.3	21:00	No	Extremely sluggish.
3.	18.22	9.56	8.66	47.5	24:40	Yes	Extremely sluggish and dry.
4.	16.62	8.50	8.12	48.8	21:15	Yes	Entirely inactive and dry.
				Bufo boreas			
1.	76.58	44.43	32.15	41.9	42:15	No	Alive, but very sluggish.
2.	65.17	36.70	28.47	43.6	39:30	Yes	Stiff and inactive.
3.	67.25	35.98	31.27	46.4	37:15	No	Slight activity, but dry; stiff.
4.	14.11	7.51	6.60	46.7	20:15	No	Slight activity, but dry; stiff.
				Bufo terrestris			
1.	19.30	11.70	7.60	39.3	20:30	Yes	Stiff; inactive.
2.	23.99	13.73	10.26	42.8	24:00	Yes	Stiff; inactive.
3.	20.87	11.88	8.99	43.0	23:00	Yes	Stiff; inactive.
4.	27.03	14.81	12.22	45.2	23:35	No	Alive, but very dry.
5.	16.18	8.63	7.55	46.6	21:00	No	Alive, but very dry.
				Hyla regilla			
1.	3.22	1.97	1.25	38.8	6:00	Yes	Inactive; stiff; quite dry.
2.	6.30	3.86	2.45	38.8	7:00	Yes	Inactive; stiff; dry.
3.	3.52	2.15	1.37	38.9	7:45	No	Dry and stiff; slight movement.
4.	3.30	2.01	1.29	39.0	7:00	Yes	Inactive; stiff.
5.	2.71	1.57	1.14	42.0	7:20	No	Alive; extremely sluggish.
6.	3.37	1.93	1.44	42.7	8:00	No	Alive; extremely sluggish.

TABLE I.—*Continued*

	1 Orig. Wt.	2 Dry Wt.	3 Loss	4 Pct. Loss	5 Time	6 Survived	7 Condition when removed
Hyla cinerea							
1.	.72	.56	.26	36.1	4:05	No	Slight movement, but very stiff.
2.	1.23	.77	.46	37.3	5:30	Yes	Very stiff and dry.
3.	1.32	.78	.54	40.9	6:00	No	Alive, but stiff and dry.
4.	.72	.41	.31	43.0	4:05	No	Alive, but stiff and dry.
Rana pipiens							
1.	33.62	23.51	10.11	30.0	19:00	Yes	Stiff; slight movement.
2.	40.58	27.12	13.46	33.1	21:45	No	Alive; very sluggish.
3.	32.96	20.89	12.07	36.6	17:15	Yes	Stiff and dry.
4.	41.48	25.32	16.16	38.9	26:50	No	Slight movement; very stiff.
5.	31.25	19.01	12.24	39.1	21:00	No	Legs moved slightly.
Rana aurora							
1.	23.18	15.82	7.36	31.7	17:00	Yes	No movement; dry and stiff.
2.	24.22	15.98	8.24	34.0	17:20	Yes	No movement; dry and stiff.
3.	25.49	16.81	8.68	34.0	18:00	No	Still alive; legs moved.
4.	24.56	15.75	8.81	35.8	18:00	No	Dry and stiff; still breathing.
5.	21.59	13.79	7.80	36.1	16:25	No	Dry and stiff; still breathing.
Rana sphenocephala							
1.	53.60	36.20	17.40	32.4	21:30	Yes	Extremely stiff and dry.
2.	53.35	35.85	17.50	32.8	22:45	No	Still alive; very stiff.
Rana grylio							
1.	62.72	46.15	16.57	26.4	24:25	Yes	Stiff and inactive.
2.	114.20	79.69	34.51	30.2	42:00	No	Stiff, but still breathing.
3.	68.84	47.99	20.85	30.2	33:10	No	Stiff, but still breathing.
4.	73.30	30.40	22.90	31.2	27:00	Yes	Entirely inactive.

degrees Centigrade, with a variation of not more than plus or minus one degree, was maintained inside the exsiccator.

The air passing into the exsiccating chamber was tested for moisture several times by placing calcium chloride in the path of the air. At no time was moisture found to be present in the air.

EXPERIMENTAL DATA

Table I represents a condensed record of the exsiccation experiments. Here, only those specimens which gave strong evidence of being at or very near their vital limit when removed from the exsiccator are mentioned, and are the only specimens used in further calculations for comparative purposes.

Most individuals of all species reacted to the experiment in a fairly uniform pattern. Usually a brief attempt was made to escape by leaping or trying to scale the walls of the glass jar. When the initial effects of the dry air were felt, however, they almost invariably settled down, drew their hind legs up to the body, their forelegs under the chin, and lowered the head. This position would tend to expose a minimum of body surface to the drying effect of the air, and possibly represents an instinctive reaction of frogs and toads to conserve body water. As exsiccation proceeded, the animals became increasingly quiescent. The skin remained visibly moist for a surprisingly long time. After a loss of 25 per cent of the body weight in water, frogs of the genera *Rana* and *Hyla* appeared as moist as when they were first placed in the exsiccator. The skin of toads, if not apparently as moist as the frogs, remained soft even when nearly a 40 per cent loss had been sustained. The approximate vital limit (the greatest water loss which could be endured before death resulted) could usually be detected by the darkened skin, the dry, shrivelled appearance, and a complete lack of activity which sometimes even extended to visible respiratory movements.

In table II, the vital limit of water loss for each species has been recorded and is expressed in two ways: (1) by the selection of a specimen of each species which survived the greatest per cent loss in body weight, and (2) the average per cent loss in body weight of those specimens which apparently reached the vital limit. Both means of expression have been derived from the data presented in column 4, table I. The first method (column 1, table II) might be considered a reliable expression of the vital limits, since in no case did a specimen of a particular species survive a greater loss of water than that recorded in this column. There is, however, a certain amount of individual variation in ability to withstand exsiccation within a species. In *Bufo boreas* for example, specimen number 1 died after a loss of 41.9 per cent of its weight, while specimen number 2 survived a loss of 43.6 per cent. Likewise in *Rana pipiens,* specimen number 3 failed to survive a loss of 33.1 per cent of its body weight whereas specimen number 4 lived after losing 36.6 per cent. For this reason, the second method, as expressed in column 2, table II, is a better expression of the vital limits for the species as a whole, since it represents more individuals, being an average of all the specimens of each species which were considered to have reached the vital limit of water loss when removed from the exsiccator. Regardless of which of these methods is used, it will be noticed that the data in the respective columns correspond very closely, in that the figures for each species are in every case almost alike. Likewise, when the species are arranged in order from those with the highest vital limits to those with the lowest, it will be seen that the sequence is alike in both cases except for the two species of *Scaphiopus,* which are so similar in either instance, that the difference between the two forms is apparently negligible.

Thus far, the water loss has been expressed in per cent of the total body weight lost. Obviously, the whole body weight of an amphibian is not made up of water, but includes a certain amount of solid material making up the tissues and organs of the body as well as bound water which cannot be driven off no matter how long exsiccation continues. The important consideration is, therefore, how much of the available water can be lost before death ensues. If one species has much

TABLE II. *The vital limits of water loss and habitats*

	1 Highest Pct. Loss Body Wt.	2 Average Pct. Loss Body Wt.	3 Highest Pct. Loss Body Water	4 Average Pct. Loss Body Water	5 Habitat
Scaphiopus holbrookii	48.1	47.9	60.5	60.2	Terrestro-fossorial
Scaphiopus hammondii	48.8	47.6	61.0	59.5	Terrestro-fossorial
Bufo boreas	43.6	44.6	54.8	55.8	Terrestrial
Bufo terrestris	43.0	43.3	54.5	54.9	Terrestrial
Hyla regilla	39.0	40.0	49.1	50.3	Terrestrial
Hyla cinerea	37.3	39.3	46.5	49.0	Terrestro-arboreal
Rana pipiens	36.6	35.5	46.3	44.9	Terrestro-semi-aquatic
Rana aurora	34.0	34.3	42.6	43.0	Semi-aquatic
Rana sphenocephala	32.4	32.6	no data		Semi-aquatic
Rana grylio	31.2	29.5	40.2	38.0	Aquatic

more body water available than another, a comparison of the per cents of total body weight lost means very little. Therefore, the water loss was expressed in per cent of body water lost (columns 3 and 4, table II) as well as per cent of body weight lost (columns 1 and 2, table II) as explained above. In order to arrive at the per cent of body water lost the amount of available water in the body had to be determined. This was done by completely exsiccating several specimens of each species (except *Rana sphenocephala,* for which an inadequate number of specimens were available) in a small, well-ventilated drying oven in which a temperature of 80 degrees Centigrade was maintained. The exsiccation was continued until a constant weight was attained for each specimen. The per cent of the body weight which was made up of water was then calculated (column 4, table III) and an average computed for each species (column 5, table III). To determine the vital limit for each species as expressed in terms of the highest per cent loss of body water (table II, column 3), the highest per cent loss of body weight (table II, column 1) was divided by the average per cent body water (table III, column 5). Likewise, to determine the average per cent loss of body water (table II, column 4), the average per cent loss of body weight (table II, column 2) was divided by the average per cent of body water present (table III, column 5).

It was found that the per cent of water in the body was very much the same for all species, ranging from 77.5 per cent in *Rana grylio* to 80.1 per cent in *Hyla cinerea* (table III, column 5). It is apparent (table II) that the order of species arranged from those with the highest vital limits to those with the lowest remains unchanged, irrespective of whether body weight or body water is used in making the calculations. It will also be noted that in the case of the two species of *Scaphiopus* the same irregularity in order occurs when the highest per cent loss of body water (column 3) is compared with the average per cent loss of body water (column 4), as when body weight was used (columns 1 and 2).

TABLE III. *Per cent of body weight composed of water*

Species		1 Orig. Wt.	2 Dry Wt.	3 Loss	4 Pct. Water	5 Ave. Pct. Water
Scaphiopus holbrookii	1.	20.24	4.34	15.90	78.5	79.5
	2.	10.07	2.05	8.02	79.6	
	3.	8.54	1.65	6.89	80.6	
Scaphiopus hammondii	1.	19.65	3.96	15.69	79.8	80.0
	2.	8.75	1.70	7.05	80.5	
	3.	17.73	3.64	14.09	79.4	
	4.	17.25	3.33	13.92	80.6	
Bufo boreas	1.	67.25	13.50	53.75	79.9	79.8
	2.	65.17	13.20	51.96	79.7	
Bufo terrestris	1.	27.03	5.92	21.11	78.0	78.8
	2.	11.65	2.56	9.09	78.0	
	3.	16.18	3.17	13.01	80.4	
Hyla regilla	1.	3.43	.68	2.75	80.1	79.4
	2.	3.01	.66	2.35	78.0	
	3.	1.89	.38	1.51	79.8	
	4.	2.45	.49	1.96	80.0	
Hyla cinerea	1.	1.32	.25	1.07	79.5	80.1
	2.	.72	.14	.58	80.5	
	3.	.72	.14	.58	80.5	
Rana pipiens	1.	40.58	8.38	32.20	79.3	78.9
	2.	41.48	9.11	32.37	78.0	
	3.	31.25	6.43	21.82	79.4	
Rana aurora	1.	8.42	1.71	6.71	79.6	79.7
	2.	4.22	.91	3.31	78.4	
	3.	15.94	2.97	12.97	81.3	
Rana sphenocephala				no data		
Rana grylio	1.	106.45	23.88	82.57	77.5	77.5
	2.	90.50	20.25	70.25	77.6	

From these observations it can be concluded that for comparative purposes, when dealing with the vital limits of water loss, it makes little difference whether the average per cent or the highest per cent loss is considered, or whether this water loss is expressed in terms of body weight or in terms of body water.

DISCUSSION

When this list of species arranged from those with the highest to those with the lowest vital limits of water loss (table II) is examined, remarkable generic differences are at once apparent. The two species of *Scaphiopus* studied endured the greatest degree of exsiccation. Within this genus it is problematic which of the two species survived the greater amount of water loss, since the average vital limit of *S. holbrookii* is only slightly greater than that of *S. hammondii,* but the highest individual vital limit of the latter species was above that for *S. holbrookii.* The two species of *Bufo* studied are also much alike, but these can endure less exsiccation than toads of the genus *Scaphiopus.* Similarly, the two species of *Hyla* are grouped together, but their vital limits are still lower than those of the bufos. The four species of *Rana* exhibit a greater range of vital limits, but they are all definitely lower than *Hyla.* Thus it is apparent that the amphibians studied reveal clear-cut generic differences in their ability to endure exsiccation, some being capable of surviving the loss of a greater portion of their body water than others.

It was thought that these differences might explain the habitat restrictions of amphibians. A survey of the various amphibians used in this study indicates that there is a gradation in habitats from those that are definitely terrestro-fossorial on the one hand to strictly aquatic on the other. As in the case of the vital limits of water loss, the differences in habitat are largely generic. For instance the two species of *Scaphiopus* are both terrestro-fossorial and it is impossible to determine which lives in the drier surroundings. However, both species are apparently adapted for a drier mode of life than the two species of *Bufo,* which are both terrestrial and again cannot be separated in regard to dryness of habitat. The two hylas are likewise difficult to separate, but both live in surroundings less dry than the bufos. All the species of *Rana* studied, with the possible exception of *pipiens,* live in moister habitats than the three genera above, although as was true of the vital limits of water loss, they show a greater range of habitats than the other genera.

In table II, each species studied is listed with its vital limit of water loss and the characterization of its habitat. It will be seen at once that there is a remarkable correspondence between the dryness of the habitats and the ability to survive exsiccation. The amphibians which have the highest vital limits of water loss are found in the driest habitats, whereas those having the lowest vital limits live in the wettest habitats.

In some instances when two species are compared, either on the basis of vital limits of water loss or habitat, the difference may be so slight as to lack significance. However, when all the species studied are considered, it can be stated that there is a distinct correlation between the habitat preferences of these amphibians and the amount of body water that can be lost without losing vitality.

Gray ('28) has shown that in vertebrates the transition from aquatic to terrestrial life was not accompanied by any serious reduction in the percentage of water present in the tissues, for in all vertebrates, irrespective of environment, the tissues contained approximately 80 per cent water. However, since terrestrial vertebrates are constantly exposed to evaporation, some mechanism for the conservation of water is necessary. This adaptation according to Gray was provided by the acquisition of a relatively impermeable skin. It was pointed out above (table III) that regardless of their habitat, the species of Amphibia studied were also made up of approximately 80 per cent water. The development of terrestrial amphibians also would necessitate some adaptation to enable them to survive considerable exposure to evaporation. Although there is very likely some difference between the permeability of the skins of various amphibian species, this adaptation alone cannot account for the ability of some species to survive a greater amount of evaporation than others, because all species studied were highly susceptible to desiccation. The evidence from the vital limits of water loss in relation to habitats appears sufficiently conclusive to state that, concerning amphibians at least, the transition to terrestrial life has been made possible to a great extent, not by the development of resistance to evaporation, but by the gradual evolution of the ability to lose a large per cent of the body water and yet survive. As an illustration, *Scaphiopus hammondii,* which occurs in semi-arid regions, lives away from open water practically the entire year. Apparently it can live in these dry areas because (among other factors) of the ability to survive a loss of almost half its body weight in water (47.6 per cent). Lacking this adaptation, it could not have survived and become established in such a dry habitat. On the other hand, *Rana grylio,* the most aquatic of the species studied, can lose only a comparatively small part of its body water (29.5 per cent) without expiring. This frog apparently remains in or near the water because its body will not stand the loss of much moisture through evaporation. Likewise, the species between these two extremes probably have been influenced in their choice of surroundings by this physiological limitation.

Therefore it may be concluded that one of the important factors which has effected the transition of amphibians from aquatic to terrestrial ways of life has been the development of the ability to survive a progressively greater loss of body water.

SUMMARY

Specimens of 10 amphibian species were exposed to the effects of evaporation and the vital limit of water loss was determined for each species.

Four different means of expression were employed in designating the vital limits of water loss. When the ten species were arranged in order from those with the highest vital limits to those with the lowest, that order remained essentially unchanged, regardless of which means of expression was used.

After a study of the habitats of the amphibians concerned and a comparison of the habitats and vital limits of water loss, it was found that a distinct correlation existed between the habitat preferences and the amount of body water that could be lost without losing vitality.

The transition from the aquatic to the terrestrial mode of life among amphibians must involve some adaptation to cope with evaporation of body water. The acquisition of a relatively impermeable skin by terrestrial species could not alone account for their ability to survive evaporation, because all species studied were highly susceptible to desiccation. It is therefore proposed that the transition to terrestrial life among amphibians has been made possible to a great extent, not by the acquisition of resistance to evaporation, but by the development of the ability to survive a progressively greater loss of body water.

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POLLEN RECORDS FROM LAKES IN ANOKA COUNTY, MINNESOTA: A STUDY ON METHODS OF SAMPLING[1, 2]

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Pollen analyses have assumed increasing significance in the study of past vegetation on our continent, and so it necessarily becomes more and more important that methods be examined critically. Characteristics of pollen grains and the laboratory procedures followed in their preparation for analysis have been studied with the aim of determining their reliability, but the trustworthiness of collecting methods and the type of instrument used in sampling have, to the authors' knowledge, had little critical consideration. Yet, conclusions dealing with lengths of time during which early successional stages of forests prevailed are so much determined by completeness of the core that the present study seemed necessary to discover to what extent sampling errors were perhaps warping the accuracy of our conclusions. Presented here is one phase of a study on methods of sampling, begun by the authors three years ago.

In the early life of a lake in glaciated areas the soil on adjacent uplands, for lack of protecting plant cover, plays a larger part in determining the nature of sediments in the lake than it does later, especially if the soil consists primarily of sand. Frequently much fine wind-blown or water-carried sand comes to rest on the coarser, less washed sand, gravel or rock which formed the original lake bottom. It is a well known fact that the Davis borer and the cylinder borer with movable sleeve jam readily in sandy deposits. At most, one can secure only one foot-level sample of sand with them unless various difficult manipulations are added to the process of boring. Since pollen workers, expressed or by inference, have interpreted levels of sediments as synonymous with length of time during which a given forest type dominated, incomplete cores introduce significant errors. Therefore, in regions where the early sediments are composed primarily of fine sand, and pollen of the pioneer forest trees is embedded in it, it becomes almost mandatory that samples from such sandy layers be included in the core.

The authors were first made conscious of this defect in cores while studying sediments from Tippecanoe Lake in Indiana ('41) where pollen was present in twelve foot-levels of sand, and in the study of sediments from Third Sister Lake, Michigan where *Picea* pollen was found in eight foot-levels of fine sand. This discovery suggested the necessity of further

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[1] This is contribution 143 from the botanical laboratories of Butler University, Indianapolis, Indiana. The field work involved in the study was made possible by a grant (No. 531) from the American Philosophical Society. We express our sincere thanks for this aid.

[2] Sincere appreciation is expressed to Messrs. S. G. Holden, Charles M. Johnson, R. L. Olson and Mrs. Ben. Forshblade for permission to camp on their property while the boring work was in progress; to Mr. S. G. Holden for information on the forest cover of Anoka County; to Messrs. Robert Wilson and Raymond Luebke for assistance in the handling and transfer of machinery and equipment, and to Mr. H. E. Blewett, Anoka County engineer, for information and maps. To Miss Jane L. Goodlet, assistant in the Department of Botany at Butler University, we are indebted for the lettering on the graphs.

investigation of the problem. We know of no place where sand is so prominent in areas adjacent to lakes and bogs as in the Anoka Sand Plain region in Minnesota, and so a study of lakes in that region was planned with the new Wilson ('41) sampler which operates efficiently even in sandy layers. Also, a previous study there of bog sediments, based on samples taken with the sleeve-type borer, made a comparison of the older and newer sampling techniques easier. Another problem grew out of the fact that in many profiles from the bogs of Anoka County *Pinus* showed an unusually high percentage of pollen in topmost levels while *Quercus* occupied a minor role (at times only 10 per cent). This does not harmonize with the impression one receives from the vegetation at present, for *Quercus* is very prominent. A comparison was made of pollen records from lakes with those from bogs to see if possible changes in vegetation following closing of the bog mat might not be represented in the recent lake deposits, and so clear the seeming contradiction.

TOPOGRAPHIC HISTORY OF THE COUNTY

The excellent description by Cooper ('35) of the glacial activity which resulted in the Anoka Sand Plain ought to be read if the interesting history of Anoka County is to be understood fully. In his opinion 70 per cent of the county should be included in the Sand Plain. Leverett and Sanderson (as quoted by Cooper, '35) classified the plain as a dunes area, assuming that the sand had been transported from the Mississippi, Elk and Rum rivers. However, results of a careful study forced Cooper to the conclusion that the "Plain in general exhibits no evidence of aeolian origin; dune forms are found only in limited areas, comprising 6 per cent of the whole." He expressed the opinion that the region is an outwash plain, occupying the interior of the territory invaded by the Grantsburg Sublobe, a transitory part of the Des Moines lobe of Late Wisconsin glaciation.

THE LAKES AND BOG STUDIED

The lakes were selected with the aim that the linear distance covered (about 35 miles), running from northeast to southwest, would involve the greater part of the county. It was later decided to include a bog in the study in order to try to secure samples in sand below those levels available to the punch and movable-sleeve type borers. The small, almost perfectly round Bethel Bog seemed excellently adapted for such an experiment, especially since a previous study here showed the *Picea-Abies* period wanting.

Crooked Lake

Crooked Lake is located in R.24 W., T.31 N., Sec. 4, T.32 N., Sec. 33. It is the southernmost of a group. Most of its shoreline is filling with organic sediments which are invaded by rooted aquatics. The bay-like outlet of the lake is filled almost completely with sediments on which *Typha latifolia* and tall grasses form a dense stand. The slope of the basin is from north to south, and the boring was made in the deepest southeast corner (24 feet of water). Three feet of extremely fine pollen-bearing sand rests on a deep layer of coarse sand. Of the latter we secured samples from fifteen foot-levels, but no pollen was found in these samples. The vegetation on adjacent sandy uplands has been disturbed greatly, and only scattered small groves of *Quercus* persist.

Ham Lake

Ham Lake is located in R.23 W., T.32 N., Sec. 16, 17, 20 and 21. This lake, too, is filling centripetally from the shores. A belt of rooted aquatics extends lakeward for a considerable distance. The southern section apparently was the deepest part of the depression, and still has the greatest depth of water. Six feet of fine pollen-bearing sand rests on coarse sand, and the total depth of sediment at the point of sampling is thirty-three feet.

Cultural influences have removed most of the forest except small groves of *Quercus* and some *Larix laricina* in a boggy border along the southeastern shore.

Bethel Bog

Along highway 65 in R.23 W., T.33 N., Sec. 5 is one of the most beautiful little bogs the authors have ever seen. High, steep slopes rise from the mat, now almost covered with *Chamaedaphne calyculata.* Considerable time was spent making trial borings to determine somewhat the general contour of the floor, so that a boring could be made in the deepest portion of the basin. Most of the fill was about seven and one-half feet in depth, except in a small central portion where fourteen feet of peat was encountered. Five feet of fine pollen-bearing sand was overlying coarse sand. By the method to be described later we were able to obtain samples also in these sandy layers.

Island Lake

Twenty-five years ago Island Lake had a greater expanse of water than at present. A drainage ditch to Martin Lake then lowered its level, transforming the island from which the lake derived its name into a part of the flanking shore. It is located in R.22 W., T.33 N., Sections 4, 5, 8 and 9. This lake is skirted by sandy shores covered with a thin layer of organic sediments. Mr. Holden, whose farm borders on the lake, told us that the northern portion of Island Lake before drainage was covered by a luxuriant growth of wild rice. The land above the old shoreline is wooded with dense stands of young *Quercus* in which scattered stems of *Pinus strobus* persist as relics. An open stand of *Larix laricina, Pinus strobus* and several species of *Quercus* covers the recently exposed 200-foot wide terrace. Near the center of the present lake, where one core was taken, eight feet of fine pollen-bearing sand capped coarser sand. Sediment totaled forty feet.

Tamarack Lake

This body of water is a fine example of a lake in the last stages of filling. The whole area is a vast rice field. *Zizania aquatica* almost completely fills the four feet of water with tangled roots and fallen culms. The 30- to 40-foot wide quaky border mat is overgrown with *Typha latifolia* and *Phragmites communis.* Thirty-six feet of sediment overlies the original lake bottom, of which four feet is represented by the same type of fine sand found in the lower levels of all Anoka County lakes and the one bog examined. Location of the lake is R.22 W., T.33 N., Sections 3, 4, 9 and 10.

METHODS OF SAMPLING [8]

In lake sediments

One of the authors (Wilson, '41) has described in considerable detail the type of apparatus, its construction and the methods followed in securing cores of sediments from lakes with open water. A brief review is included here for the convenience of the reader, and because of the important part the technique plays in the results presented.

A float consisting of a platform lying across two boats or supported by oil drums, or a combination of both, is built. A 15- to 20-foot boom pole, held in position by guy-ropes, is erected near the center of the float. From it a pulley is suspended, over which a ½-inch hose can run. A chain hoist is also attached to the top of the boom with which to pull casing. Use of casing becomes a necessity when working in deep water. A hoop fastened near the top of the boom is an excellent support for long lengths of idle pipe. A water force pump is mounted on the floor of the float and connected to the ½-inch hose. Drilling operations are carried out through a small hole near the center of the float.

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[8] Preparation of sediments for analysis followed the Geisler ('35) method. In general, two hundred pollen grains of tree genera were counted for each foot-level. Variations from this procedure are indicated in table I.

Several techniques are involved in making a boring, depending on the nature and depth of the sediment. However, all samples are taken in short, usually foot-long increments. The small amount of material actually saved for pollen analysis is removed from the center of the bottom part of each core segment. This eliminates any possibility of contamination from sediments at higher levels. Samples from the soft flocculent upper part of a deposit are obtained with a one-foot long tubular sampler (1¼-inch bore) which has a modified iris diaphragm mounted on the lower end. The diaphragm can be closed by rotating the sampler after it has been forced one foot into the undisturbed sediment. Fins mounted on two rings encircling the sampler activate the diaphragm lever. To obtain samples below the first foot-level, water is pumped through the sampler as it is being pushed into the sediment. The jet of water forced out of the lower end of the apparatus by this operation not only washes away the sediment in its path but keeps the sampler clean. When the desired level for a sample is reached pumping must be halted; the hose is detached and the sampler is pushed one foot into the undisturbed sediment. This process is effective through the soft and moderately consolidated sediment of the topmost twenty to thirty feet. A valve placed just above the sampler, which opens when the pump is running but is closed at other times, supports the hydrostatic pressure in the ½-inch pipe by which the sampler is lowered and raised. In compact deposits it is more convenient, and in sediment over thirty feet deep necessary, to put down a casing through which the operations are carried out. It acts as a support for the ½-inch pipe to which the sampler is attached. It also guides the sampler into the same hole each time it is being lowered for a sample. Standard 1¼-inch pipe is ordinarily used for casing. It is put into position by attaching the hose to the top and forcing water out of the bottom as it is being lowered into the sediment to the desired level. When working through a casing, a sampler with ¾-inch bore is the maximum size which can be used. The diaphragm is omitted in such operations. It is not needed, since compact sediment (except sand) will be held in the pipe by sidewall friction.

In sand a sampler with ½-inch bore is used. Such an instrument gives a higher ratio of sidewall contact per unit of volume of sediments than larger samplers. If samples of sandy layers are taken in three- to five-foot increments they will usually stay in the pipe. The best way to fill the sampler with sand is repeatedly to raise it a few inches and jab it down with considerable force, thus pushing new and lower increments of sediment into the pipe with each jab. Two persons stationed on opposite sides of the pipe, and jabbing simultaneously, can carry out the process most effectively. With a little experience this technique makes it possible to obtain a sample of the same length as the depth of sediment penetrated by the sampler with approximately the same increment of sand from each foot-level. Extremely fine sand may at times be too compacted to permit penetration by the jabbing method, but a sample can be secured by pounding the ½-inch pipe to which the sampler is attached with a sledge hammer. The blows must fall on a piece of wood laid on the pipe to avoid crystallizing the metal. Sand is most easily removed from the instrument by tapping it with a hammer. Attaching the sampler directly to the hose and maintaining a high pressure with the force pump also aids in pushing the sand out of the pipe, which can easily be placed in order on a clean sheet of waxed paper as a long undisturbed core segment.

Taking samples in sandy sediments of bogs

The procedure for securing the pollen-bearing sand in Bethel Bog where no water was available to apply the washing

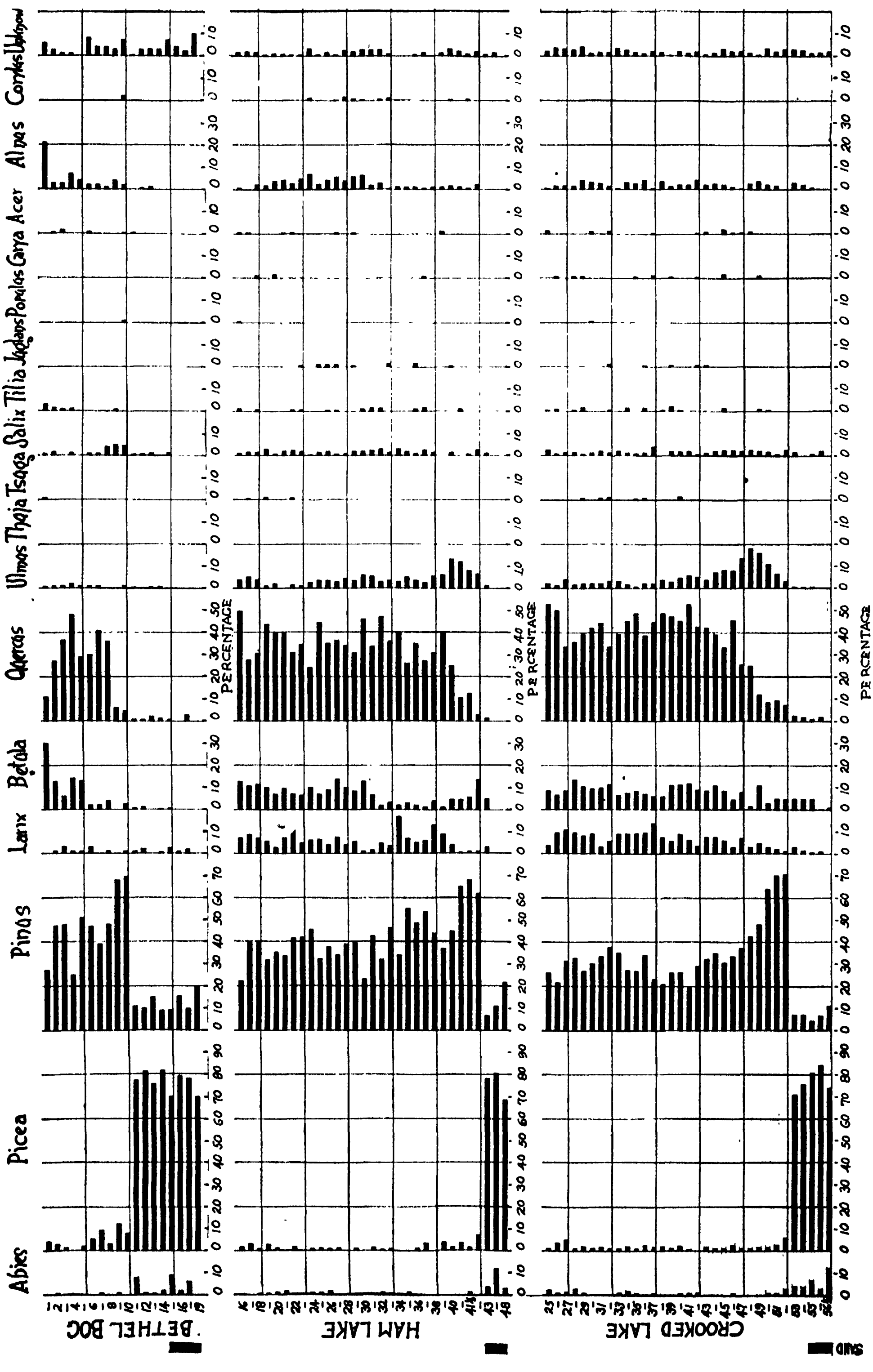

FIG. 1. Pollen profiles from Bethel Bog, Ham and Crooked lakes, Anoka County, Minnesota.

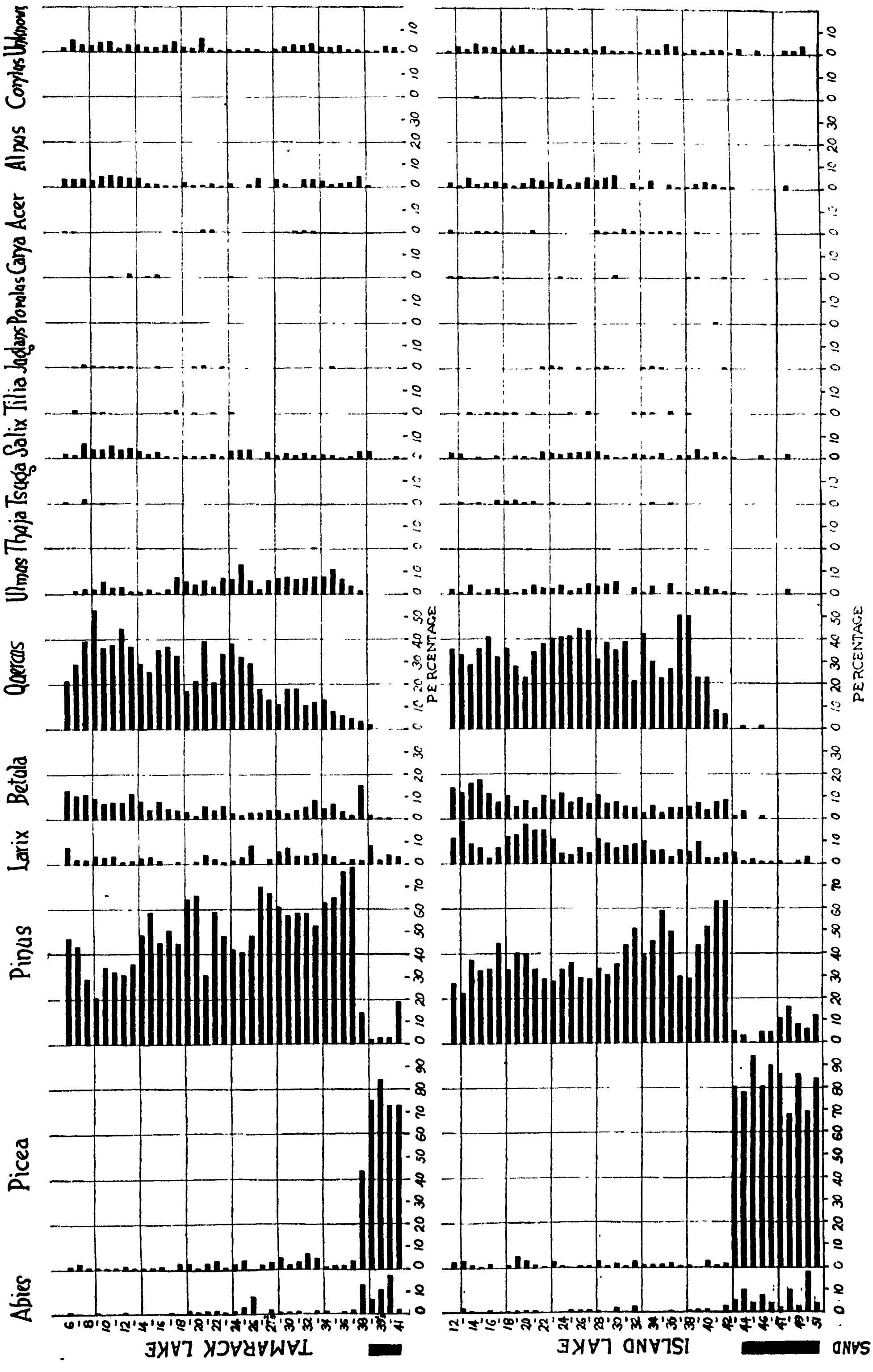

Fig. 2. Pollen profiles from Tamarack and Island lakes, Anoka County, Minnesota.

method described above, and where ordinary bog borers could not function, was as follows: A core of the overlying peat was removed down to the sand with a regular peat borer. A snugly-fitting cork was placed into the bottom of an ordinary ½-inch pipe which was then lowered through the hole in the peat to the level of the sand. The closed end prevented picking up peat as the pipe was being lowered. The cork and sediment then were forced into the pipe by the previously described jabbing or pounding methods. Since the field work reported in this paper was carried out one of the authors, by the method just described, has successfully secured samples of very fine sand through a thickness of fifty feet.

Characteristics of Lake Sediments

The constitution of sediments in these Minnesota lakes is variable to a high degree, ranging from sand to peat to high grade marl. The whole range was found in all the lakes, but no correlation appears to exist between the lakes in the order of arrangement of these sediment types. This suggests strongly that edaphic rather than climatic factors were controlling in determining the type of sediment deposited at any particular time and place. That the various types of sediments differ in the time necessary for their accumulation is obvious, and this makes correlation of thickness of sediment with time a difficult problem. For example, some sediments imbibe considerable water, forming a jelly, while others retain relatively little water. The former obviously accumulate at a faster rate than the latter. Also, when a lake does not produce enough acid to re-dissolve the carbonates sinking to the bottom it will certainly fill at a more rapid rate than at periods when it does. Where frequent alteration occurred in the types of sediment laid down in a given body of water, as in the lakes described here, it is a questionable procedure to asume an equal rate of accretion per unit of time. Detailed consideration will be given this problem in another paper.

Results

The profiles of the five lakes are very similar in the major features of vegetational change which they record. All record an important *Picea* or *Picea-Abies* dominance at the beginning of succession. The *Picea* period persisted for a long time in southeastern Minnesota (based on depth of accumulated sediments). The number of feet of sediment indicating an almost complete dominance by Picea is very similar to that in Indiana bogs located in regions where clay or loam soil constitute the flanking uplands. A very important *Pinus* dominance replaced *Picea,* which continued while two to three foot-levels were laid down, except at Tamarack Lake where the *Pinus* period was evident in eleven foot-levels. *Pinus* was superseded by a *Pinus-Quercus* association which has persisted with fluctuations in importance of the two genera for a long time. With the exception of those from Tamarack Lake and Bethel Bog, the profiles show a decided increase in *Quercus* in the upper one or two foot-levels. *Ulmus* was most abundant during the *Pinus* period and declined with the ascendency of *Quercus. Betula* and *Larix* show increasing importance at levels above the close of the *Picea* period (figures 1 and 2). Pollen of grasses increases in abundance towards the topmost levels except at Bethel Bog, where the peak occurs in the sector between the five- and eight-foot levels (table I). Grass pollen was most abundant in the sediments from the more northern Island and Tamarack lakes. The latter is a vast rice field and the former was noted for the same feature twenty-five years ago. The pollen resembles that of *Zizania aquatica,* but it could belong to *Andropogon furcatus* or *Sorghastrum nutans,* since the pollen of these three species is very similar in size and structure of the pore. Foot-levels recording *Picea* dominance would have been reduced considerably, or eliminated entirely, if the layers of fine sand had been omitted in the boring.

TABLE I. *Pollen grains of grasses tabulated at a given foot-level while 200 pollen grains of woody genera were counted. A count of less than 200 grains is indicated in parentheses*

Foot-levels	Bethel Bog	Tamarack Lake	Island Lake	Ham Lake	Crooked Lake
1	6	water	water	water	water
2	16				
3	18				
4	9(100)				
5	45(100)				
6	57(100)	185			
7	40(100)	214			
8	73(100)	176			
9	—(100)	309			
10	33	195			
11	9	36			
12	2	69	185		
13	5	63	190		
14	1	52	11		
15	4(150)	57	13		
16	1(100)	39	12	74	
17	—(50)	56	5	36	
18	—	62	14	26	
19	—(10)	43	12	20	
20		31	18	14	
21		38(100)	40	31	
22		52	39	45	
23		32(175)	44	28	
24		56	47	33	
25		19(100)	63	24	61
26		22(100)	53	29	55
27		22(100)	49	24	82
28		37(100)	63	31	36
29		36	21	51	57
30		36	35	35	18
31		37	26	21	23
32		27	47	29	39
33		26	24	68	37
34		23	33	28(100)	38
35		37	38	23(100)	41
36		29	43	43	29
37		7	42	39(150)	48
38		8	31	46(1 0)	48
39		8	37	26(100)	44
40		3	12	25	45
41		5(100)	12	11	60
42			5	9	40
43			2	6	38

From 44 to 56.5 foot-levels for Crooked Lake, number of pollen grains were respectively as follows: 50–37–42–35–39–42–26–12–25–14–3–9–1–21(100).

TABLE II. *Number of foot-levels in profiles from bogs and lakes in Indiana and Minnesota showing* Picea *or* Picea-Abies *control*

Indiana			Minnesota		
	Sand	Loam		Sand omitted	Sand included
Old Lake Barlow		7	Bethel Bog		6
Bacon's Swamp		19	Crooked Lake		5
Jeff Bog		7	Ham Lake		6
Kokomo Bog		13	Island Lake		9
Mill Creek Bog		8	Tamarack Lake		4
Otterbein Bog		7	Cedar Creek Bog	1⅓	
Round Lake Bog		4	Coon Creek Bog	3¼	
Silver Lake Bog		7	Coon Lake Bog	2⅔	
Yountsville Bog		13	Elk River Bog	2	
Lake Cicott Bog	2		Grassy Lake Bog	1⅓	
Lakeville Bog	2		Ham Lake Bog	2	
Shipshewana Bog	3		Karmel Bog	2	
			Linwood Bog	1⅓	
			Princeton Bog	4	
			Rice Lake	3¼	

DISCUSSION

Pollen profiles from sediments of still-existing lakes are in many respects more reliable in their records than those from bogs. This is particularly true for profiles from shallow bogs, where the upper end is likely to be truncated. The Wilson sampler is superior to any others used by the authors because it is not limited in operation by sandy layers. This feature is of extreme importance where the adjacent land mass is primarily sand, which became the source of almost all sediment laid down in the early history of the lake. If one checks over Indiana reports on pollen profiles, it appears that failure to sample sandy layers might be the cause of low numbers of foot-levels recording *Picea-Abies* control (table II). The profiles from depressions in sandy regions may record all vegetational changes but the time for the *Picea* period will be truncated if some pollen-bearing sandy layers are not sampled. This difference is very apparent when a comparison is made between lake profiles reported here and those by Artist ('39) from bogs of Anoka County (table II). The bog profiles show a *Picea* dominance in 1.5 to 4 feet of sediment, while those from the lakes show the boreal forest control in four to nine feet of sediment. His records agree well with duration of the *Picea* period shown in pollen profiles from sandy regions in Indiana, or with the writers' Anoka County lake records when all but one foot-level sample of sandy deposits are eliminated from the latter (table II). Such truncated profiles give the impression that *Quercus* was a very early and prominent invader of the region, which in reality is not true. It seems obvious that both the Indiana records from bogs in sandy regions and Artist's Anoka Sand Plain bog profiles have foot-levels omitted because of the inability of the Davis or movable-sleeve type borers to penetrate into such sediments.

The manner of accumulation of the sedimentary sandy layers is still an unsolved problem. When we referred to them as "wind-blown" sand we pictured a short transfer by wind of fine dust-like quartz particles from the sandy shores to the water or to the ice in autumn and winter. The fact that the particles are angular does not necessarily rule out transport by wind. Twenhofel ('39) said that the deposits by aeolian agencies do not always consist of rounded particles when the transfer was short. McKelvey ('41) described the carrying of considerable sand more than one-half mile from the shores to the deeper parts of lakes by flotation. Grains of such sand masses, however, are large, measuring from one-half to two millimeters in diameter. Seventy-nine per cent of the grains from the sandy layers sampled by the authors are only .001 to .06 millimeters in diameter, or of loess size. Some of the dry sand from the Anoka County lakes was sifted on the surface of a glass of water and most of the particles still floated after four days. Lutz ('41) found abundant wind-carried mineral matter in crevices in the bark of trees. In size it was similar to that of the particles in the sandy layers of the Minnesota lakes. There is, thus, the probability that the layers of fine sand in lakes located in sandy regions may be of aeolian origin. The manner in which the sand was transported to the lake is, however, of less significance in a pollen study than the fact that it was accumulated over a period of time after the lakes had been formed, and that pollen of pioneer trees was embedded in it. It is further an undeniable fact that the Davis and movable-sleeve type borers do not operate in such sediments; and finally, when these layers are omitted the profiles will show a truncated *Picea* period.

The significance of grass pollen, especially when it is abundant, has frequently been interpreted as indicative of reduced moisture and subsequent grassland invasion. This study produces strong evidence that increasing abundance of grass pollen (table I) in the upper foot-levels is indicative of shallowing water in the lake basin and invasion by grasses of the *Zizania aquatica* type. The surface layers of Tamarack Lake must receive abundant grass pollen from the dense cover of plants of this species flourishing there at present. We also feel that it distorts the picture of the dominant vegetation if pollens of herbs and grasses are given equal importance with those of woody genera in the percentage figures of the profile. It seems almost essential to consider them separately as we do in tabulation of stems in a forest survey, where each stratum receives its own quantitative consideration. Godwin ('40) considers even the representation of *Alnus* separately from the percentages of tree pollen, and his arguments for doing so are sound. If we had included grass pollen in the percentage figures of the profiles from Island and Tamarack lakes the trees would have received such negligible representation that one might have inferred dry climate with disappearance of forests and encroachment by prairie. In reality, however, forest is still the dominant vegetation in the region and the grass pollen is without doubt contributed by aquatic grasses which are not even competitors of trees.

Another feature considered is the difference in vegetation reflected in the upper part of the pollen profiles from lake sediments and those derived from bogs. The open surfaces of lakes are still accumulating pollen, whereas closed surfaces of bogs very likely have ceased recording, but the time of cessation is unknown. It was therefore assumed that lake sediments might show more recent climatic and vegetational changes, indicated by decline of *Pinus* and increase of *Quercus*, which spectra from bogs could not show. Profiles from seven of the thirteen bogs described by Artist ('39) show *Pinus* predominant in the uppermost foot-levels (50 to 83 per cent), while none of the thirteen profiles record *Quercus* in excess of *Pinus*. In a number of his records *Quercus* is so poorly represented that one receives the impression it had been on the decline, almost becoming extinct in the Anoka Sand Plain. The pollen spectra from the lakes place *Quercus* in a more prominent position. They also correlate well with a description of the forests given us by Mr. S. G. Holden, an old settler, whose farm is located between Island and Tamarack lakes. He said, "There was only a little commercial lumbering in the county. The southern section of Anoka County had perhaps very little pine since before the days of settlement by whites. In 1886 the school section immediately south of me, in the town of Columbus, was cut and the logs were hauled to Boot Lake. The southeastern section of Isanti County had considerable pine, and a sawmill operated at Typo Lake. Originally the forest on my land had pine, but it was scattered, as in all of Anoka County. Most of the white pine was on low ground in the wire grass marshes. Dense stands were east of Linwood Lake on so-called 'Pine Island,' also east of Coon Lake and Tamarack Lake. At Boot Lake one finds a little jack pine even to-day. After the pine was cut different kinds of oak formed the new forest cover."

With exclusion of Tamarack Lake the profiles from the lakes (figures 1 and 2) show decided increase in *Quercus* over *Pinus* in the topmost layers. Eight of the thirteen bogs investigated by Artist ('39) show *Quercus* dropping to less than 10 per cent of the total. It is apparent that the records from the bogs are incomplete, and that vegetational changes have taken place after formation of a mat ended the pollen record. Artist's Ham Lake Bog profile apparently ceased recording during the *Pinus* period. The profiles from the lakes presented in figures 1 and 2 are more regular and show not only climatic change in southeastern Minnesota during the close of the *Picea* period but another during which *Pinus* controlled most of the crown cover in the forest. A later climatic change favored the *Pinus-Quercus* complex. The important *Pinus* period is striking in forest succession in northern Indiana, as reported by Houdek ('33), Potzger and Wilson ('41), Smith ('37), Swickard ('41); in Michigan, as described by Potzger and Wilson ('41); in Wisconsin, as shown by Potzger and Richards ('42), Wilson and Galloway ('37), Potzger ('42); and eastward, in New Jersey, as reported by Potzger and Otto ('42). In northern Indiana *Quercus* replaced *Pinus* almost entirely; in New Jersey the *Pinus-Quercus* complex was enriched by the addition of *Tsuga*. In New Jersey *Quercus* and *Castanea*, during the time involved in the deposition of the topmost layers, have reduced the importance of *Pinus*. In northern Wisconsin and Michigan *Quercus* has shown barely sufficient aggression to be considered a part of the crown cover of the forests. *Pinus* evidently represents a climate which is too cold for *Quercus* to be able to establish itself as a competitor of *Pinus*, but is of sufficient moderation to enable *Pinus* to compete successfully with *Picea*.

SUMMARY

1. Pollen analyses of sediments from four lakes and one bog in the Anoka Sand Plain of southeastern Minnesota are presented.

2. The specific aim of the study was to discover what part fine sand played in pollen-bearing sediments in sandy regions, and to determine somewhat the reliability of profiles if such layers were omitted in sampling.

3. Borings were made with the new Wilson sampler in Crooked, Ham, Tamarack, and Island lakes and in Bethel Bog.

4. Very fine pollen-bearing sand constituted from three to eight feet of the

sediments overlying coarse sand. Levels showing a decided *Picea* period are doubled if the sandy layers are included in the core.

5. A method is described by which samples may be secured from sandy sediments of bogs.

6. Profiles from lake sediments in Anoka County, Minnesota show increasing prominence of *Quercus* pollen in the topmost levels. This increase in *Quercus* is not recorded in profiles from bogs of the same region. The possibility exists that bogs ceased recording before a moderation in climate favored increase in *Quercus*. However, since *Pinus* and *Quercus* fluctuated considerably in abundance for a long time after the close of the *Pinus* period, this may not be so significant as it appears. No profile from the lakes, however, contained 60 to 87 per cent of *Pinus* pollen in the topmost levels as did five of the thirteen bogs studied by Artist ('39). This points to truncated records in bogs and indicates that profiles from lakes are more reliable in regions where climatic changes have occurred in recent times.

7. Abundance of grass pollen increased decidedly in the topmost levels, especially at the more northern Tamarack and Island lakes. There is strong evidence that *Zizania aquatica* contributed most of the grass pollen. Instead of indicating a drier climate, increase in grass pollen may merely mark stages in the filling of lakes when aquatic grasses could invade.

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EFFECT OF DEPTH OF IMMERSION ON APPARENT PHOTOSYNTHESIS IN SUBMERSED VASCULAR AQUATICS[1]

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The influence of the depth of immersion on the rate of apparent photosynthesis in submersed aquatic plants has an important bearing on the ecological distribution of such species. Important inferences regarding the dynamics of photosynthesis, respiration, and perhaps other plant processes also can be drawn from the results of studies of this problem. Most investigations of the relation between depth of immersion and photosynthesis in submersed aquatics have been made with marine or freshwater algae. A few investigators, however, notably Ruttner ('26), Schomer ('34), Manning *et al.* ('38), and Meyer and Heritage ('41) have worked on this problem in vascular aquatics. This paper reports the results of an investigation upon five such species, several of which have not been used previously in such studies. The experimental technique employed in this work is believed to incorporate a number of improvements as compared with the procedure employed by previous investigators.

EXPERIMENTAL PROCEDURE

The species used in this investigation were *Potamogeton Richardsonii* (Benn.) Rydb., *Najas flexilis* (Willd.) Rostk. & Schmidt, *Anacharis canadensis* (Michx.) Planchon, *Vallisneria americana* Michx., and *Heteranthera dubia* (Jacq.) MacM.[2] Plants were collected directly from shallow parts (depths not exceeding 1 meter) of Lake Erie in the vicinity of the Stone Laboratory at Put-in-Bay, Ohio. Collections were made in the late afternoon or evening, the plants being kept overnight in a large vessel of lake water. Six samples of plant material were used in each experiment. Selected apical portions of the plants, each about 15 cm. long, were used of all the species except *Vallisneria americana.* Each sample of this species consisted of a strip cut from the apical portion of the leaf blade about 50 cm. in length. All of the samples of plant material used in any one determination were selected carefully for close uniformity in size and configuration.

Except for the final titrations (see later), all stages in each of the experiments were conducted on a barge anchored in the mile-wide channel about midway between North Bass and Middle Bass Islands, at a point where the water was 10–12 meters deep. All experiments were carried out on clear August days in 1941 between the hours of 9:00 A.M. and 3:30 P.M. (solar time) during periods when the lake surface was relatively smooth.

The exact procedure followed was adopted only after an extensive and critical experimental study of the suitability of the methods for use in an investigation of the type described in this paper. Since the results of the investigation on the technique of measuring rates of apparent photosynthesis in submersed aquatics will be published as a separate paper no attempt will be made in the following discussion to justify or evaluate the exact procedure followed.

Pyrex culture tubes, 3 cm. in diameter and 20 cm. in length, with a capacity of 130 ± 1 ml., were employed as containers for the plants during all experiments. Each tube was provided with a tightfitting rubber stopper, hollowed on the under side to prevent accumulation of air bubbles at that point when the tube was stoppered, and a short, tapered glass plug which fitted the hole in the stopper snugly.

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[1] Paper from the Franz Theodore Stone Laboratory and the Department of Botany, No. 457, of the Ohio State University.

[2] Nomenclature follows Fassett, N. C. A manual of aquatic plants. New York. 1940.

The tubes required for an experimental run were filled in the laboratory with Lake Erie water of reduced and uniform oxygen content, and stoppered in such a manner that no air bubbles were entrapped in the tubes. The actual oxygen content of the water as used was about half that of water at the same temperature in equilibrium with the partial pressure of oxygen in the atmosphere; expressed in usual units the oxygen content of the water used was about 4 p.p.m. or about 3 ml. per liter. The oxygen content of the water used varied slightly from one experiment to another, but all the tubes used in any one experiment were filled with water of exactly the same oxygen content. Use of water with an oxygen content less than the saturation value was necessary in order to prevent emission of gas bubbles from the plants when high rates of photosynthesis were attained. This would invalidate the method used for measurement of the oxygen content of the water, which determines dissolved oxygen only.

The plants therefore were immersed during the experiments in a water medium identical with that in which they grew in nature except that its oxygen content had been reduced to about half the usual value. The following are pertinent data[3] regarding the physical and chemical properties of Lake Erie water at a depth of 1 meter as determined in August, 1942: temperature 22.7 — 26.3° C., dissolved oxygen 8.0 — 8.2 p.p.m., free carbon dioxide 0 p.p.m., carbonate concentration 2.0 — 5.0 p.p.m. (in terms $CaCO_3$), bicarbonate concentration 79.8 — 84.0 p.p.m. (in terms $CaCO_3$), pH value 8.4 — 8.5. None of these properties of Lake Erie water in the Bass Island region show any great variation at this season from the values given for depths up to 10 meters.

At the beginning of an experimental run a sample of plant material was transferred to each of six tubes of water prepared as previously described. All of the tubes of water used in these experiments previously had been brought to the temperature of the lake water by first immersing them in the lake for a suitable period of time. The tubes were restoppered without entrapping any air bubbles within them. The plants had been kept until this time out of direct sunlight. The tubes were fastened to a specially constructed wooden float which, when placed in the water, held them in a horizontal position at a depth of 0.05 meter under the surface of the water. The purpose of this preliminary run was to allow time for the completion of the photosynthetic induction period, if any, and to bring the plants into equilibrium with the reduced oxygen concentration of the water.

At the end of 30 minutes the float was removed from the lake and the plants quickly transferred to a second set of tubes. These tubes also were attached to the float and immersed in the lake in the same manner and at the same depth as during the first run. The purpose of this "calibration run" was to determine the rate of apparent photosynthesis in all of the samples of plant material while they were exposed to identical environmental conditions.

At the end of this second 30-minute period the float was again removed from the lake and the plants transferred to the third set of tubes. These tubes were attached to a weighted wire cable in such a manner that, when the cable was lowered into the water, one of the tubes was in a horizontal position at each of the following depths below the surface: 0.05, 2, 4, 6, 8, and 10 meters. The top tube in this experimental run was at the same depth (0.05 meter) below the surface of the lake as all of the tubes in the calibration run. The duration of the experimental run was also 30 minutes. (In the experiment on *Heteranthera dubia* all three of the successive runs were 40 minutes in length instead of the usual 30 minutes.)

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[3] Analysis made by Dr. D. C. Chandler.

The complete transfer of a set of six plants from one set of tubes to the next was accomplished in about 5 minutes. No individual plant, however, was exposed to the air for more than a few seconds during such transfers. Removal or introduction of plants from or into the tubes always was accomplished with as little disturbance as possible of the enclosed water. As soon as the tubes were removed from the water at the ends of the second and third runs they were wrapped immediately in black cloths which remained in place until the plants were removed which was accomplished within a few minutes. Likewise, prior to each of these runs, as soon as the plant had been introduced into a tube, it was wrapped in a black cloth which was left in place for the few minutes which intervened before the tubes were immersed in the lake.

Immediately after removal of the plants from the tubes at the ends of the calibration and experimental runs the necessary reagents for determination of the oxygen content of the water by the Winkler method were added to each tube and to check tubes which contained samples of the water used. The procedure outlined in Standard Methods for the Analysis of Water and Sewage, 7th Ed. 1933, was followed, except that a 0.0125 *N* solution of sodium thiosulfate was used for the final titration. One milliliter of such a solution is equivalent to 0.07 ml. of oxygen at standard conditions. Preliminary studies indicated that it was unnecessary to use the Rideal-Stewart modification of the Winkler method in this work. Actual titrations, on 100 ml. aliquots from each tube, including the check tubes, were carried out after the tubes had been brought back to the laboratory. From these data the increase or decrease in oxygen content per 100 ml. of water could be computed for each tube in which the plants had been immersed.

The temperature of the lake water was measured at depths of 0.05 and 10 meters during each experimental run with a suitable "minimum" thermometer.

Measurements of light intensity, incident on a horizontal surface, were made with the degree of accuracy obtainable with a Weston "Photronic" cell when used in lacustrine habitats. The cell was mounted in a metal case and provided with an opal glass filter according to the specifications of Atkins *et al.* ('38). The electrical circuit from the photocell to suitable milli- and microammeters was completed through a heavy waterproof cable which also served as a support for the instrument while it was suspended in the water. Although instruments of this type are being used rather widely for measuring the penetration of light into water, not more than a roughly quantitative significance should be attached to results obtained with them. This is particularly likely to be true in bodies of water in which rapidly fluctuating turbidities are often encountered. This is the situation in that part of Lake Erie in which these investigations were conducted. Photocells of the rectifier type are all selective detectors of radiant energy, and since both quality and intensity of light vary with depth of immersion, strictly quantitative relations between the intensity of light prevailing at a given depth under the water and the current developed by the cell are not to be expected.

The light intensity measurements recorded in this paper were all made during the "experimental run" of each series of determinations. The highest value of any reading recorded was 735 microamperes for the reading in air on August 7, at 10:45 A.M.; the corresponding reading obtained with the recording pyrheliometer located at the Stone Laboratory about one and one-half miles distant was 1.23 g.-cal. per cm.^{2} per minute. This reading was given an arbitrary value of 100 and all light intensities are expressed

TABLE I. *Apparent photosynthesis in* Anacharis canadensis *at different depths*

August 21, 1941 Water temperature, 21° C.

Plant no.	Calibration run 9:19–9:49 A.M. Gain O_2, ml. per 100 ml. solution	Experimental run 9:53–10:23 A.M.		Relative light intensity. Air, 97	Expt. run as per cent of calib. run
		Depth of tubes, meters	Gain or loss O_2, ml. per 100 ml. solution		
1	0.198	0.05	0.171	89	87
2	0.209	2	0.141	38	68
3	0.238	4	0.050	12	21
4	0.213	6	0.029	3.5	14
5	0.246	8	0.019	1.0	8
6	0.140	10	−0.019	0.27	−14

on a relative basis with reference to this as a standard.

RESULTS AND DISCUSSION

Two or more experiments were performed with plants of each of the five species reported on in this paper. Closely similar results were obtained in all of the determinations on a given species; hence the one set of data presented for each species may be regarded as representative.

If six similar portions of plants of the same species are suspended at different depths beneath the surface of a body of water and their measured rates of apparent photosynthesis found to be different there is no way of ascertaining to what extent differences in the observed rates result from differences in environmental conditions and to what extent they arise from intrinsic differences in the photosynthetic capacity of the several samples of plant material. For this reason the photosynthetic rates of all the plants used in a given experiment first were measured under identical environmental conditions in the calibration run before their rates of apparent photosynthesis were measured at different depths. "Calibration" of plants in this manner gave a quantitative measurement of their inherent differences in photosynthetic capacity. In other experiments we have found that the rate of apparent photosynthesis in several species of submersed aquatics remains virtually constant for periods of at least several hours under constant environmental conditions as favorable to photosynthesis as any likely to be encountered in Lake Erie. Gessner ('37) obtained similar results with *Ceratophyllum demersum.* Hence it is a valid inference that differences in the rate of apparent photosynthesis exhibited by the plants in the experimental as compared to the calibration run result from differences in

TABLE II. *Apparent photosynthesis in* Najas flexilis *at different depths*

August 2, 1941 Water temperature, 25° C.

Plant no.	Calibration run 2:25–2:55 P.M. Gain O_2, ml. per 100 ml. solution	Experimental run 3:01–3:31 P.M.		Relative light intensity. Air, 94	Expt. run as per cent of calib. run
		Depth of tubes, meters	Gain or loss O_2, ml. per 100 ml. solution		
1	0.173	0.05	0.152	87	87
2	0.160	2	0.105	57	66
3	0.139	4	0.054	26	39
4	0.209	6	0.020	8.4	10
5	0.134	8	0.006	2.8	4
6	0.114	10	−0.030	0.82	−26

the environmental conditions at the different depths. In order to obtain comparable indices of the rate of apparent photosynthesis (photosynthesis minus respiration) the oxygen evolution for each plant during the experimental run has been expressed as the percentage of the oxygen evolution during its calibration run.

Except for occasional short periods the portion of Lake Erie in the vicinity of the Bass Islands is virtually an isothermal body of water. Actual measurements during the course of these experiments never showed a temperature differential of more than 1° C. between the 0.05 and 10 meter depths, and usually less than this. Any differences found in the rate of apparent photosynthesis at different depths cannot, therefore, be ascribed to the temperature factor. This essentially isothermal condition of the lake simplifies interpretation of the results of an investigation of this type.

The conditions under which these experiments were performed were such that any differences found in the rate of apparent photosynthesis at one depth as compared with another must result principally and probably entirely from differences in the light conditions at the different depths. As is well known, both the intensity and quality of light vary with depth of penetration into water. No attempt was made in this investigation to evaluate effects of differences in light quality at different depths upon the rate of apparent photosynthesis. Even the measurements of light intensity, recorded in connection with the measurements of photosynthesis, can be accepted only with certain qualifications, as pointed out previously.

The results obtained with *Anacharis canadensis* (table I) indicate that there is a consistent decrease in rate of apparent photosynthesis with increase in depth. The compensation point was attained in this species under the prevailing environmental conditions at a depth of between 8 and 10 meters.

Results obtained with *Najas flexilis* (table II) are, in general, similar to those obtained with *Anacharis canadensis*. The light intensities at all except the 0.05 meter depth were greater in this series than in any other. This was correlated with the lesser turbidity of the water on this date than on other days on which experiments were performed. The compensation point for this species appears to be slightly higher than for any of the other species investigated.

The results obtained with *Potamogeton Richardsonii* (table III) were similar to those found with *Anacharis canadensis* and *Najas flexilis*. In general, rate of apparent photosynthesis decreased consistently with increase in depth of immersion of the plants. The compensation point was closely approached, although not quite reached at the depth of 10 meters. Light intensities at the different depths in this experiment were closely compar-

TABLE III. *Apparent photosynthesis in* Potamogeton Richardsonii *at different depths*

August 20, 1941 Water temperature, 22° C.

Plant no.	Calibration run 2:19–2:49 P.M. Gain O_2, ml. per 100 ml. solution	Experimental run 2:55–3:25 P.M.		Relative light intensity. Air, 92	Expt. run as per cent of calib. run
		Depth of tubes, meters	Gain or loss O_2, ml. per 100 ml. solution		
1	0.393	0.05	0.317	81	81
2	0.367	2	0.233	36	64
3	0.428	4	0.138	10	32
4	0.346	6	0.077	2.5	22
5	0.361	8	0.068	0.95	19
6	0.368	10	0.040	0.41	11

TABLE IV. *Apparent photosynthesis in* Vallisneria americana *at different depths*

August 23, 1941 Water temperature, 22.5° C.

Plant no.	Calibration run 2:11–2:41 P.M. Gain O_2, ml. per 100 ml. solution	Experimental run 2:46–3:24 P.M.		Relative light intensity. Air, 91	Expt. run as per cent of calib. run
		Depth of tubes, meters	Gain or loss, O_2, ml. per 100 ml. solution		
1	0.191	0.05	0.191	83	100
2	0.183	2	0.136	33	74
3	0.225	4	0.115	13	51
4	0.207	6	0.081	4.1	39
5	0.154	8	0.048	1.4	31
6	0.186	10	0.047	0.54	25

able with those prevailing during the experiment with *Anacharis canadensis.*

The relation between depth of immersion and rate of apparent photosynthesis was distinctly different in *Vallisneria americana* (table IV) than in the other species studied. Although there was a consistent decrease in rate of apparent photosynthesis with increase in depth of immersion a very appreciable rate (25 per cent of that at the surface) was maintained at a depth of 10 meters, although the prevailing light intensity was only of the order of 0.5 per cent of that at the surface on the clearest days.

Results of the experiments on *Heteranthera dubia* (table V) were also somewhat distinctive. The rate of apparent photosynthesis is the same at the 2-meter depth as at the surface, but there is an abrupt and marked diminution in rate between the 2 and 4 meter depths. Rates were essentially the same at the 4, 6, and 8 meter depths although this vertical range corresponds to a considerable range of light intensities. The compensation point was attained between the depths of 8 and 10 meters.

In all five of the species studied the rate of apparent photosynthesis decreases less rapidly with depth of immersion than does the light intensity. This is in accord with the principle, apparently valid for all species of plants, that maximum photosynthesis per unit of leaf area is attained at light intensities which are considerably less than that of full sunlight.

For all the species studied, except *Najas flexilis,* the compensation point is less than 2 per cent of full sunlight on clear August days. The compensation point for *Najas flexilis* apparently falls between 2 and 3 per cent of full sunlight. In an analogous investigation with *Ceratophyllum demersum,* in which similar experimental methods were used, it was found by Meyer and Heritage ('41) that in this species also there is a consistent decrease in the rate of apparent photosynthesis with increase in depth, and that the compensation point had a value of less than 2 per cent of full sunlight intensity in August. The compensation points found for these aquatic species are considerably lower than the values which have been recorded for most species of terrestrial plants with the exception of a few pronounced "shade" species.

The depth of penetration of sunlight into the water during the period of this investigation approached closely to the maximum values which have been recorded for Lake Erie water in the Bass Island region (Chandler, '42). Hence some approximate predictions can be made regarding the depth to which the several species investigated might be expected to survive. No species will survive at a light intensity corresponding to the compensation point, because under such conditions sufficient photosynthesis occurs to compensate for respiration only during the period of illumination. Bare survival should be possible, however, at

TABLE V. *Apparent photosynthesis in* Heteranthera dubia *at different depths*

August 7, 1941 — Water temperature, 24° C.

Plant no.	Calibration run 9:13–9:53 A.M. Gain O_2, ml. per 100 ml. solution	Experimental run 9:57–10:37 A.M. Depth of tubes, meters	Experimental run 9:57–10:37 A.M. Gain or loss O_2, ml. per 100 ml. solution	Relative light intensity. Air, 100	Expt. run as per cent of calib. run
1	0.238	0.05	0.240	93	101
2	0.268	2	0.279	51	104
3	0.252	4	0.038	18	15
4	0.273	6	0.034	5.7	12
5	0.244	8	0.035	1.8	14
6	0.307	10	−0.030	0.68	−10

light intensities not greatly exceeding the compensation point, although still greater intensities would be required if the plant is to thrive and grow. Examination of the data in tables I–V suggests that all the species except possibly *Najas flexilis* could survive, although not necessarily grow, at depths down to about 8 meters, under conditions permitting approximately maximum penetration of light into the waters of western Lake Erie. It also seems probable, judging from the results with this species, that *Vallisneria americana* could survive at somewhat greater depths than the other four species investigated. The results suggest that this species falls into a somewhat different category ecologically than the other four.

Because of season to season and often day to day variations in turbidity, light penetration into Lake Erie water is often quantitatively much less than during the period of this investigation. Actually, therefore, the limiting effect of such periods of lower light intensity would make survival of these species unachievable at as great a depth as might be possible were light penetration to be maintained consistently at the values which prevailed during this investigation.

SUMMARY

A study has been made of the relative rates of apparent photosynthesis in *Potamogeton Richardsonii, Najas flexilis, Anacharis canadensis, Vallisneria americana,* and *Heteranthera dubia* when immersed at a series of depths ranging to 10 meters in Lake Erie. In all five species the rate of apparent photosynthesis decreases less rapidly with depth of immersion than does the light intensity. In all of these species except *Najas flexilis,* for which the value is slightly higher, the compensation point is less than 2 per cent of the sunlight intensity on clear summer days. The results indicate that *Vallisneria americana* can survive at lower light intensities than any of the other four species.

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NOTES AND COMMENT

PARABIOSIS IN NEOTROPICAL "ANT GARDENS"

The famous psychiatrist and myrmecologist, Professor August Forel, coined the term "parabiosis" in 1898 to denote the association between two species of ants living together in Colombia which he had found during 1896. Workers of the two species (*Dolichoderus debilis parabiotica* Forel and *Crematogaster limata parabiotica* Forel) formed common files to and from feeding grounds and a common nest, although they maintained sepatate chambers for their brood. This symbiosis differs from the more common type whereby compound nests of several species are formed, in which the chambers of each may anastomose with those of the other but are not confluent. In such cases the ants do not associate together and are frequently hostile. Parabiosis differs from another commoner association where ants of one species live with another in varying degrees of parasitism.

Ule described in 1901 what he called ant gardens which he had studied the previous year in Brazil. These gardens were balls of earth around small trees at variable heights above the ground from which grew a definite flora of small plants belonging to the families Araceae, Bromeliaceae, Gesneriaceae, Moraceae, Piperaceae and Cactaceae. Invariably the balls of earth were inhabited by one of several species of ants (*Camponotus femoratus* Fabr., *Azteca traili* Emery, *A. olitrix* Forel, *A. ulei* Forel). His far-fetched later conclusions that the ants deliberately sowed the seeds of the plants in earth which they brought up from the ground to make the balls were correctly criticized by Wheeler ('21).

Wheeler also showed that in British Guiana these ant gardens with the same or a similar flora were commonly inhabited by two species of ants, the *Camponotus femoratus* and Forel's *Crematogaster limata parabiotica*, living together in parabiosis. His paper contains a valuable review of Forel's, Ule's and Mann's examples of parabiosis in Colombia and Brazil.

In 1935 I was able to examine the ant gardens in exactly the same part of British Guiana where Dr. Wheeler's studies were conducted. During that year and the next, I found similar ant gardens in two countries not hitherto known to contain these ants and their gardens, Venezuela and Surinam. In addition to finding the *Camponotus* and *Crematogaster* so associated, a third member of the biocoenose was discovered, a tiny yellow species of *Solenopsis*. The greater complexity of the biocoenose was also shown by the discovery of phorid flies ovipositing in the adult worker ant bodies and the finding of a peculiar larval insect and adult weevil in one garden.

Camponotus femoratus, the largest and principal worker of the ant garden, was described by Fabricius in 1804 (*Syst. Piez.* p. 397) and in 1862 by Roger (*Berl, Ent. Zeitschr.* 6: 284). It is recorded only from the basin of the Amazon in Brazil and from the junction of the Cuyuni and Mazaruni rivers in British Guiana. The following records in my collection are new:

Venezuela: Rio Araturi and SE border of Orinoco Delta, Feb. 6 and 8, 1935 (N. A. W.).

British Guiana: Forest Settlement, Mazaruni R., Aug. and Sept. 1935 (N. A. W.); 22½ mi. west of Kartabo Point, 7·ix·1935 (N. A. W.); Oronoque R. of Courantyne drainage, July and Aug. 1936 (N. A. W.); Waikarabi Creek, Barama R., 28·iii·35 (J. G. Myers 5023); Mataruki, Upper Essequebo R., 5·xii·35 (J. G. M. 5835); Upper Essequebo, 1·xii·35 (J. G. M. 5788); Watershed between Essequebo and New R., 6·xii·35 (J. G. M. 5841).

Surinam: Above Wanoceri Falls, Courantyne R., 14·vii·36 (N. A. W.).

Trinidad, B. W. I.: Maracas Valley, 23·iii·35 (N. A. W.); Rio Claro, 3·i·35 (N. A. W.).

My records are all from tropical rain forest. The ants, however, were found in various types: swamp rain forest, white sand thin forest and virgin greenheart forest (*Ocotea Rodioei* (Schomb.)) in B. Guiana; both high forest and largely cultivated forest of a cacao plantation in Trinidad; Guianan rain forest and mangrove (probably *Rhizophora mangle* L.) in Venezuela. This ant was called "Warumuri" by an intelligent Arawak Indian guide and helper in B. Guiana.

Crematogaster limata was described by F. Smith in 1858 (*Cat. Hym. Brit. Mus.* 6: 139) and the subspecies *parabiotica* by Forel in 1904 (*Zool. Jahrb. Syst.* 20: 683). Forel described two varieties later. The species and its forms are recorded from Brazil, British Guiana, Colombia and Panama. The following records in my collection are new:

Venezuela: SE border of Orinoco Delta, 6·ii·1935 (N. A. W.).

British Guiana: the Forest Settlement, 22½ mi. W of Kartabo Point and Oronoque R. records listed for *Camponotus femoratus* above.

Surinam: the Wanoceri Falls record listed above.

The hitherto unrecorded third ant in the biocoenose is tiny (2 mm. in extended length) and yellow in color. It belongs to a new species of *Solenopsis* near *S. helena* and *pollux* to which the name, *S. parabiotica* Weber, may be applied (Weber, '43). The ants were found in three gardens near the Forest Settlement, Mazaruni R., British Guiana and doubtless would have been found in more, here and elsewhere, had more time been available for examination.

DESCRIPTION OF THE GARDENS

The *Camponotus-Crematogaster* gardens are described by Wheeler as "varying from the size of a walnut or orange to that of a football," but larger gardens were seen at heights of 50–100 feet above the ground. These latter were not examined. Gardens of similar size were seen in 1935 in the same area and those which I examined varied in diameter from 6 cm. to 23 cm. Most were somewhat elongated, the largest being 66 × 23 cm. The average dimensions of five were 30 × 16 cm., being elongated about the branch or trunk of the tree and the development of new chambers could probably continue to a considerable extent up and down the stem. The height above ground of the five nests varied from 1.6 to 6 meters with an average of nearly 4 meters.

A garden on the Surinam side of the Courantyne River above Wanoceri Falls was 15 × 5 cm. but this was noted as smaller than most of the nests glimpsed while traveling up this river. A garden near the junction of the Oronoque and New Rivers in the far interior of British Guiana was 20 cm. in diameter.

Small plants commonly grow from the gardens. Ule collected from the gardens in Brazil inhabited solely by *Camponotus femoratus* the following: *Philodendron myrmecophilum* Engl., *Anthurium scolopendrinum* Kunth., var. *poiteananum* Engl., *Streptocalyx angustifolius* Meg., *Aaechmea spicata* Mait., *Peperomia nematostachya* Link, *Codonanthe uleana* Fritsch, and *Phyllocactus phyllanthus* Link. From gardens inhabited by three species of *Azteca* in Brazil he collected *Philodendron myrmecophilum* Engl., *Nidularium myrmecophilum* Ule, *Ficus myrmecophila* Warb., *Marckea formicarum* Damm., *Ectozoma ulei* Damm., *Codonanthe formicarum* Ule, and two undescribed species of Gesneriaceae. "These fourteen species belonged to such different families as the Araceae, Bromeliaceae, Gesneriaceae, Moraceae, Piperaceae and Cactaceae."

Those plants identified by Wheeler and Bailey belonged to the Gesneriaceae ("probably species of *Streptocalyx* and *Codonanthe*") and "an *Anthurium*, a *Peperomia* and a few Bromeliads."

One plant impressed me at the time as being particularly characteristic of these gardens and was seen not only at the Forest Settlement but also 22½ miles west of Kartabo Pt. in B. Guiana and in that part of the Orinoco Delta, Venezuela, belonging to Venezuelan Guiana (Fig. 1). An Arawak Indian referred to it by the name "Kobua." As many as six stems of what may have belonged to one plant would be growing from even the small gardens. Specimens in flowers (collected 3·ix·1935) were brought to Harvard University and submitted to Dr. L. B. Smith who pronounced them to belong to the species *Codananthe calcaratus* (Miq.). The flowers in life were white with a five-petalled tubular corolla and a pinkish or lavender throat which was spotted. The unidentified species of Gesneriaceae figured by Wheeler (p. 97) may have been this *Codonanthe*. The roots of this and other plants ramified through the carton of the gardens and served to assist in binding it into a firm nest. Ule maintained that the ants deliberately sowed seeds of the plants characteristically growing from the gardens but I agree with Wheeler in considering such behavior not proved. Rather it more safely may be considered that seeds of these plants, lodging at random in the gardens or accidentally carried in by the ants as they might any particle of similar size, germinate and develop because the garden affords a suitable environment. In this biocoenose the ants would profit by the root growth of the plants adding to the firmness of the nest while the plants would be protected by the ants from *Atta, Acromyrmex* and other arthropod pests.

Far from being merely soil brought in by the ants or lodged by wind or gravity among the roots, the material used in constructing the garden has a definite carton consistency like that fabricated by *Crematogaster* and *Camponotus* ants of many species or by some species of *Nasutitermes* termites (Figs. 1, 2). The base of the carton appears to be humus or decomposed plant remains adhering to the roots of epiphytes, the bark of the tree and in similar places in the neighborhood of the nest. As an ant carries such a particle in its mouth salivary secretions may well be absorbed by the material and assist in the cementing of it into carton. Soil lodged at random by the wind may be ruled out of consideration since winds and wind-blown dust are rare in rain forests; material lodged by gravity similarly is probably unimportant.

The ant chambers were highly irregular in form and size (Fig. 2). An occasional one would be as large as 40 × 10 mm. Partitions between chambers were thin so that a large proportion of the garden was available for nesting purposes. Chambers of the *Crematogaster* and *Camponotus* anastomosed freely while the *Solenopsis* nested in minute cells in the partitions and had entrances into the far larger chambers of the other ants. In one garden the *Solenopsis* chambers were found in central, basal and peripheral portions. In another garden their chambers were chiefly in the peripheral portions. In a third the cells were seen only between the carton and stems of plants growing from the garden. Generally speaking the medial chambers were largest and were occupied by the *Campo-*

notus but frequently small chambers of Crematogasters occurred here also. While cutting down one garden *Camponotus* workers ran off and upon investigation of the nest only Crematogasters were found. These had a huge number of females and much brood, the latter roughly separated in separate cells into piles of eggs, larvae and pupae. In this nest only comparatively small cells were present and it is possible that it was a new nest, perhaps an offshoot of one growing on a neighboring tree 60 cm. away, and that the Crematogasters had initiated it. Two weeks later another nest was found which was occupied largely by the *Crematogaster* and *Solenopsis* with few *Camponotus* workers present. It was thought at the time that the *Camponotus* might be moving to a nearby garden. In a third garden the Crematogasters were much more numerous than the *Camponotus* and occupied by themselves, in addition to the usual chambers throughout the nest, a little external mass of carton, on the outside of which dried leaves were attached.

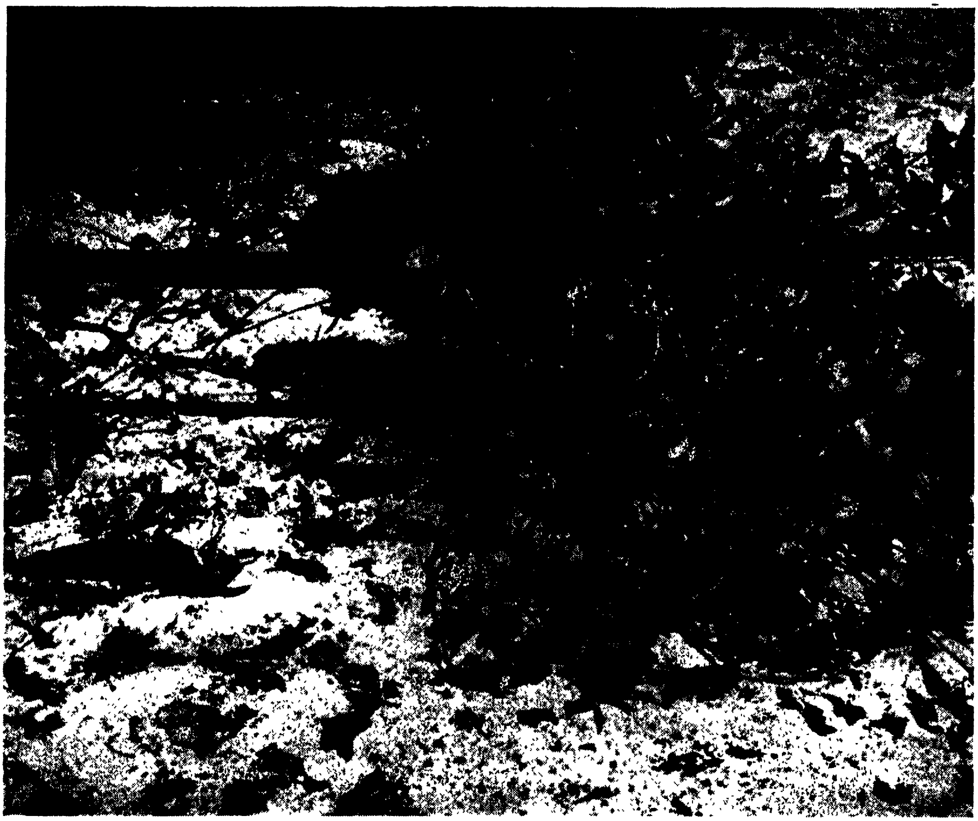

Fig. 1. Ant garden attached to recently felled tree, containing *Camponotus femoratus* Fabr. and *Crematogaster limata parabiotica* Forel ants living in parabiosis. Characteristic plant growing from garden is *Codonanthe calcaratus* (Miq.). Forest Settlement, British Guiana. N. A. Weber, phot.

BEHAVIOR OF THE ANTS

Both the *Camponotus* and *Crematogaster* ants are aggressive, rushing forth from the nest as soon as it is disturbed and viciously attacking the intruder. The *Camponotus* are much the larger and have strong mandibles but no sting. Like other formicine ants they bite and curve forward the tip of the abdomen to spray the wound with formic acid so that a person may form a hasty impression of being stung. The *Crematogasters,* although small, are so numerous, active and vicious as to be as annoying as the *Camponotus.* They possess a sting too small to pierce the human skin in most exposed places, unless given plenty of time, but a bite that may be felt. This aggressive behavior, however, is not always constant. In one nest the *Camponotus* ants were most aggressive, coming out to attack at the slightest disturbance, while the *Crematogasters* remained inside. When cutting down another nest the *Camponotus* ran from the vicinity and only *Crematogasters* were found inside.

FIG. 2. The same garden dissected. *Camponotus* ants leaving the garden and frenziedly crawling over the white sand were killed by the sun and heat in less than two minutes.

One garden with particularly aggressive *Camponotus* ants was cut down at eleven A.M. and placed on white sand of the thin forest floor, in a spot where the sun penetrated, in order to photograph. The sand was so hot that I could barely hold my hand on it and the intensity of the reflected sunlight was almost unendurable. Perspiration ran freely off me while merely standing in the clearing. The sun and heat quickly killed the *Camponotus* which frenziedly ran from the nest and exposed themselves on the sand. One worker which ran quickly from the nest over the sand started kicking on its back in 1¼ minutes and in another quarter minute was dead. Many other ants were killed in a similar interval.

Both species tolerate the *Solenopsis*. These tiny ants could walk unmolested by the larger species. None of the three ants was seen to attack another member of the trio, the *Solenopsis* treated the others as part of the environment while the larger ants acted as two castes of a polymorphic species.

PHORID PARASITES AND OTHER MEMBERS OF THE BIOCENOSE

Several nests in the Forest Settlement, Guiana area were seen parasitized by phorid flies.[1] These flies were seen to oviposit on both *Camponotus* and *Crematogaster* workers, temporarily paralyzing the ants. As the flies hovered over the ants, even some centimeters distant, the ants reacted in a characteristic manner. The *Camponotus* reared up on their legs or else vibrated jerkily as do *Lasius americanus* and many other ants. The Crematogasters generally up-ended their triangular gasters or else raised the fore parts of the body in a threatening manner. Neither ant manifested the frenzy or terror-like attitude of *Atta* soldiers and workers which have often been watched while attacked by phorids. The flies appeared to attempt oviposition on the petiole, or gaster, or junction between these segments. They ignored the tiny *Solenopsis* workers, which would probably not have enough food to feed the larval fly, and the brood of all three ants.

A myrmecophilous beetle was found in one *Crematogaster* cell which contained ant brood. This beetle, weevil-like in appearance, had numerous clavate, glandular-appearing hairs. In the same nest a peculiar larva was taken. Projecting from the pronotum were two dense circlets of clavate, glandular appearing structures. Interspersed were long hairs which also protruded in circlets from the dorso-lateral margins of each segment.

SUMMARY

Forel in 1898 coined the term parabiosis to denote an association of two species of ants in Colombia which formed common files to and from feeding grounds and a common nest, although they maintained separate chambers for their brood. Ant gardens, balls of earthy carton formed by ants about trunks of trees, were described first by Ule in Brazil in 1901. One of several species of ants inhabited the gardens and a flora of certain small species of herbaceous plants always grew from them. Ant gardens were found in 1920 by Wheeler in British Guiana inhabited by two species of ants, *Camponotus femoratus* Fabr. which was taken in the Brazilian ant gardens, and *Crematogaster limata parabiotica* Forel which was one of the parabiotic species in Colombia. The author in 1935–36 found these gardens in Venezuela, British Guiana and Surinam inhabited by the same *Camponotus* and *Crematogaster* ants. In addition a third and minute ant, *Solenopsis parabiotica* Weber, was found living in the thin partitions between chambers of the larger species. Phorid flies parasitized the *Camponotus* and *Crematogaster* and two other myrmecophiles were found. The characteristic plant growing from the gardens was identified as *Codonanthe calcaratus* (Miq.). The aggressive behavior of the larger ants and the tolerance of all three towards one another are described.

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[1] Representative specimens are in the hands of Professor C. T. Brues for determination.

AN EFFECTIVE METHOD OF DIAGRAMMING DIURNAL MOVEMENTS OF ZOÖPLANKTON ORGANISMS[1]

Although there is a very large literature concerned with the daily vertical movements of zooplankton organisms, the significance of data contained in many of these papers has been minimized because of the fact that unsuitable tabular or graphic methods have been used. The devices most commonly employed may be conveniently classified according to the following categories:

1. Numerical tables. This is perhaps the simplest way of presenting diurnal migration data. The numbers of organisms collected at the various depths are usually indicated in a series of vertical columns which are arranged according to the time of collection (table I).
2. Several types of histograms. One of the most common diagrams of this type involves vertical series of horizontal bars, each series comprising the samples taken at a particular time, and the length of each bar corresponding to the number of organisms found in a particular sample taken at a particular depth (figure 1). A modification of this device is sometimes used where the length of each bar corresponds to the *percentage* of the total number of organisms collected in all of the samples comprising each vertical series. Sometimes, instead of bars, a vertical axis of symmetry is used for each series, with the various widths corresponding to the numbers of animals found at the particular depths.
3. Curves representing the daily movements of the *average individual* in a population (figure 2).[2]

While all of these methods are quite satisfactory for demonstrating the migrations of large populations of zoöplankters which exhibit pronounced daily vertical movements, they are not particularly suitable for showing the diurnal movements of small populations of Rotatoria, Cladocera, and Copepoda, especially those species which are characterized by slow, vertical "drifts" of relatively small amplitude. Moreover, it seems important that diurnal migration data should be presented in a manner which can be easily and quickly interpreted by the average reader interested in ecological phenomena.

Weighty tabular material is particularly unsuitable for the presentation of "drift" data, because of the fact that the large amount of numerical material necessarily used often obscures small population movements and must be examined closely by the average reader before proper interpretations can be made. Similarly, it is often difficult to interpret series of histograms, particularly when an inappropriate scale is used, when the vertical distribution is relatively homogeneous or unusually irregular, or when there are small numbers of organisms present in the collections. Curves representing the migrations of "average" individuals, on the other hand, may be actually misleading because of the fact that they do not indicate the general vertical distribution plan of the *entire* population at any one time.

The method which is here outlined, however, was devised in order to minimize some of these difficulties, so that even "drift" data could be presented in a manner readily interpreted. This method, which is well-adapted to plankton trap catches and involves the use of quartile curves, is outlined in the following paragraph.

By arranging the cumulated numbers of organisms in a vertical column for each series of samples, the quartiles may be easily established in the usual way. For the series of samples taken at noon, August 3, 1940, in Summit Lake, Colorado (see table I), for example, the cumulated numbers are as follows:

Depth, meters	Cumulated numbers of organisms
0	1
1	1
3	4
5	16
7	21
9	24
11	38
13	43
(13.6)	(48)

Although the deepest sample was taken at 13.0 meters, it is arbitrarily assumed, for the sake of completeness, that there were as many organisms actually at the bottom (13.6 meters) as there were in the deepest sample. It is easily seen that the quartiles fall between 3.0 and 5.0 meters, at 9.0 meters, and between 9.0 and 11.0 meters. By interpolation, they can be shown to lie at 4.3, 9.0, and 10.7 meters. In other words, at noon, 25 per cent of the organisms were

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[1] Contribution No. 5, Limnological Laboratory, Biology Department, University of Colorado. Field work associated with this paper was made possible through grants from the Penrose Fund of the American Philosophical Society and the Graduate School Research Fund of the University of Colorado. The writer gratefully acknowledges this aid.

[2] The method for deriving such curves is given by E. B. Worthington. 1931. Vertical movements of fresh-water macroplankton. *Int. Rev.*, **25**: 394–436. Incidentally, Worthington's equation has been misprinted; it should read:

$$\text{Average depth} = \frac{x^1d^1 + x^2d^2 + \cdots}{x^1 + x^2 + \cdots}.$$

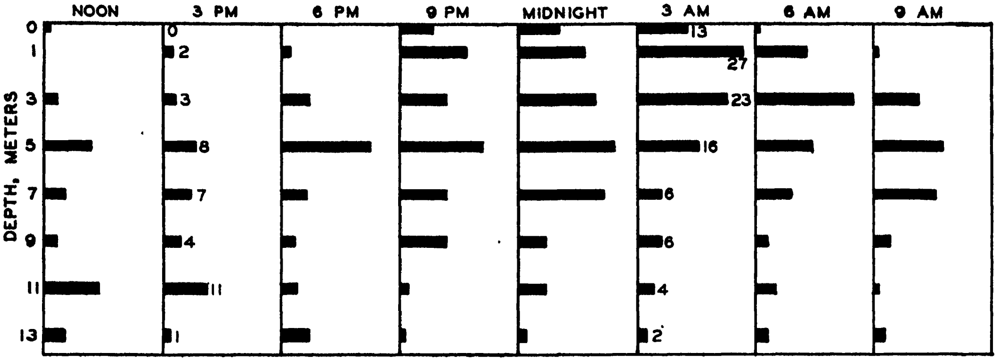

FIG. 1. Diurnal migration of *Daphnia pulex* in Summit Lake, Colorado, August 3 and 4, 1940. Actual numbers of organisms per ten-liter plankton trap sample have been inserted for 3 P.M. and 3 A.M.

between the surface and 4.3 meters, 25 per cent were between 4.3 and 9.0 meters, the third quarter between 9.0 and 10.7 meters, and the bottom quarter were between 10.7 and 13.6 meters. The three points, 4.3, 9.0, and 10.7 meters, are then indicated in the final diagram. In a similar manner the quartiles may be determined for each vertical series of samples. In the completed diagram (figure 3) the final quartile curves have been drawn in.

The use of three curves, dividing the population into equal quarters, is simply an arbitrary device. Two curves, or four or more, may be used, as desired, depending on the density of the population, the frequency of sampling, and the depth of the body of water.

Perhaps the outstanding objection to using this method of diagramming diurnal migration is the fact that considerable time is involved in manipulating and preparing the data for presentation in final form. The writer has found, however, that with a little practice, a large amount of data can be handled in a surprisingly short time. A second objection is that the final diagram does not give any idea of the *actual numbers* of organisms involved. This objection may be easily disposed of, however, by simply inserting the numbers of organisms collected per unit volume of water for one or more vertical series of zoöplankton samples. Such data have been inserted in figure 3 for the vertical series taken at 3 P.M. and 3 A.M.

Two other objections may be noted. First, the use of quartile curves does not take into account numerical irregularities in zoöplankton populations in the water between any two successive sampling depths in a vertical series. Second, this method is not particularly accurate when only small numbers of organisms are present in a body of water. Both of these objections are inherent mechanical collecting difficulties in

TABLE I. *Vertical distribution of* Daphnia pulex *in Summit Lake, Colorado, August 3 and 4, 1940. Expressed as numbers of organisms per ten liters of water*

Depth, meters	Time							
	noon	3 P.M.	6 P.M.	9 P.M.	mid-night	3 A.M.	6 A.M.	9 A.M.
0	1	0	0	8	10	13	1	0
1	0	2	2	17	17	27	13	1
3	3	3	7	12	20	23	25	12
5	12	8	23	21	25	16	15	18
7	5	7	6	12	22	6	9	16
9	3	4	3	12	7	6	3	4
11	14	11	4	2	7	4	5	1
13	5	1	7	1	2	2	3	3

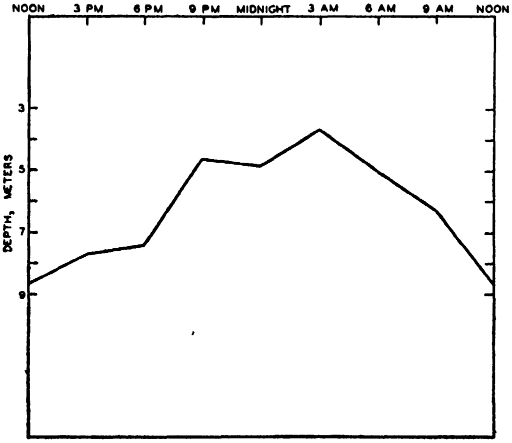

FIG. 2. Diurnal movements of the average individual of *Paphnia pulex* in Summit Lake, Colorado, August 3 and 4, 1940.

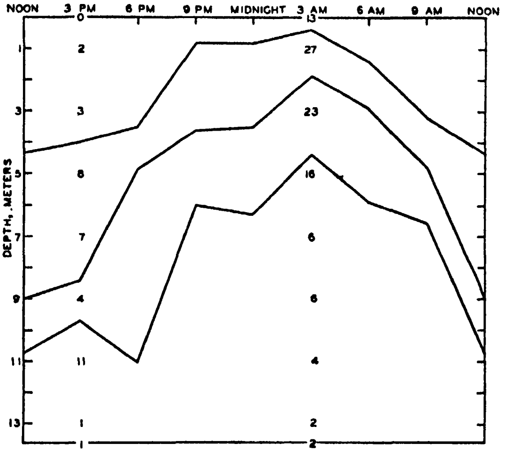

FIG. 3. Quartile curves showing the diurnal movements of *Daphnia pulex* in Summit Lake, Colorado, August 3 and 4, 1940. Actual numbers of organisms per ten-liter plankton trap sample have been inserted for 3 P.M. and 3 A.M.

the field, however, and cannot be satisfactorily overcome regardless of the manner in which the data are treated. The only obvious remedy is to make sure that the plankton samples are taken at frequent depth and time intervals so that the results will more closely approach true significance.

The advantages of using such a system for demonstrating diurnal migration are obvious from a comparison of table I and figures 1, 2, and 3, all of which were constructed from the same raw data. Whereas the other methods require a certain amount of study, figure 3 can be quickly understood and interpreted. It shows much more plainly and compactly than the other devices the general vertical distribution of the entire population, as well as the speed of vertical migration as indicated by the slope of the individual curves. Furthermore, it shows, without disproportionate exaggeration, relatively slight movements and tendencies of the population as a whole. These can be seen in table I and figure 1 only after a more careful examination. Lastly, in conjunction with the curves, the picture is made more apparent by the use of specific collection data for representative vertical series of samples.

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NOTES ON THE BASILISK AT BARRO COLORADO ISLAND, CANAL ZONE

The most conspicuous lizard on Barro Colorado is *Basiliscus basiliscus.* It is abundant along the shore and to a lesser degree in the ravines along the numerous small streams flowing into Gatum Lake. The island is densely wooded except for a few small clearings. The shoreline is very irregular, resulting in a large number of coves where beaches are practically nonexistent and the forest extends to the water's edge. The writer spent a few weeks during July and August of 1938 observing the Basilisks in a cove just to the north of the laboratory inlet and clearing. Previous observations (Park, '38; Park, Barden and Williams, '40) have reported the general activity of animals on this island and the cove was chosen for its accessibility rather than for an unusual concentration of Basilisks. It was forested to the water's edge except for about 50 feet at one end. At the head of the cove two small streams flowed in, as well as a number of lesser streams along the sides. It was hoped that the number of Basilisks might be determined and the extent of their movements and possibly some evidences of territoriality found.

As a first step the shoreline was divided into 50-foot strips and a numbered marker placed at each 50-foot interval. As thus measured the cove shoreline was 2100 feet long and roughly V-shaped in outline, the distance across the opening of the V being about 500 feet. It was essential to mark the lizards so that they could be identified when seen again. A considerable amount of time was spent at first in trying to noose the lizards. With the aid of another person to handle the noose while the writer paddled, two lizards were finally captured. Another Basilisk was taken by hand at night as it slept in the hollow top of a stub located in the water. Alone, the writer was not able to control the cayuco and at the same time successfully manipulate a long pole with a noose at the end, so noosing was abandoned in favor of marking the animals with white paint. At first a rather primitive method was employed, consisting of dipping a wad of cotton in the paint and shooting it at the lizards with a slingshot. An improvement over this was the use of a rubber bulb to squirt paint at the lizards. This allowed more accurate shots at a distance of 20 feet. If a lizard was missed, it would frequently remain undisturbed for a second shot. If a hit was made, the markings were quickly noted with the aid of binoculars and recorded along with the position as determined by means of the numbered markers.

By these various methods 23 lizards were marked distinctively. Of this number four were not seen again; the others were seen from 1 to 10 times. During the course of the observations 28 trips were made by cayuco around the cove. The greatest distance any Basilisk was recorded from the original place of marking was 105 feet. Most of them were seen where first marked or within 15 or 20 feet. The greatest period between date of marking and last date seen was 22 days. This was recorded for lizard No. 2, an immature which was captured on July 18th at night as it was sleeping in the hollow top of a stub which projected two feet out of the water and was located opposite station 1390, about 15 feet from shore. The lizard was taken back to the laboratory, banded with white adhesive tape, and released the next day at the point of capture. It was seen again on July 21, at 1290, July 29 at 1390 (again asleep in the stub), and August 9 at 1290. Actually, the animal did not have to move 100 feet to go from 1290 to 1390 because these points were at the head of the cove and the lizard could easily swim or run across the water. When released after banding, this lizard ran over the surface of the water about 10 feet to a floating log, then turned and came back past the boat, running about 30 feet on the water, or half the distance to shore. Then it settled low in the water and swam most of the remaining distance and finally submerged completely. I did not see it land but noted it on several later occasions as mentioned above.

It is my impression that young lizards when alarmed were much more likely than the adults to attempt to escape by running over the surface of the water. Perhaps the greater weight of the adults in proportion to the area available for contact with the water—only the hind feet are employed—makes this feat more difficult for the adults. I am privileged to quote from a letter from Dr. E. R. Dunn in this connection. On August 2, 1923, while making a crossing of a branch of the Guabo River, on the Atlantic slope of Panama in Bocas del Toro Province, Dr. Dunn, Mr. Chester Duryea and three Chiriquano guides "chased a young *Basiliscus plumifrons* out over the shallow water. After running some distance, it took to swimming and diving and went below the surface and hid, in water not more than a foot deep. We circled around and waited. We were able to see it hiding on the bottom, partly concealed among stones, before we took up scattered positions and waited for it to emerge. After about ten minutes it swam to the surface, and then got up on top of the water and ran about 20 feet to the shore."

During the day the lizards were seen on the ground or in trees, lianas or bushes within a few feet of the ground and not far from the water. A path through the woods parallel to the shore was cut and it was observed that the Basilisks were almost wholly restricted to a strip about 15 or 20 feet from the water's edge. Night trips around the cove revealed no lizards sleeping in what were their favored spots during the day. These positions or "perches" were apparently for resting or sunning for the lizards showed little activity there. It was a puzzle as to when they fed. It seemed likely that they secured their food early in the morning or followed a policy of watchful waiting during the day for food to come within reach. A combination of these two methods seems most likely. On two occasions small Basilisks were found asleep at night on horizontal branches about three feet from the ground.

The largest number of Basilisks seen during one tour of the cove (2100 feet) was 24. Of these 8 were marked and 16 unmarked. On this date 16 lizards had already been marked. From this and similar data I estimated the population of Basilisks for the cove to be about 40 or 45 or one lizard per 50 feet of shoreline. This latter figure can be used to estimate roughly the Basilisk population for the island, since as already noted the lizards appear to favor a relatively narrow area along the shoreline and along the streams in the ravines. Although the area of Barro Colorado is only 6.6 square miles, the shoreline is about 40 miles long. This would give over 4200 Basilisks for the island as a minimum, plus a smaller number for those along the streams, which I have no data for estimating.

The adult male Basilisk is readily recognized because of the crest on the occipital region of the head and the crest on the back, extending part way down the tail. The females and immature males lack the crest. Of the total of 23 lizards marked, three were definitely males, five were females, five were undoubtedly females (probably included some immature males) and ten were immature, the smallest being about five inches in total length.

As to territoriality, no evidence, such as defense of a certain area of shoreline, was noticed, but the time available for study was too short to allow the drawing of any conclusions as to its presence or absence in *Basiliscus basiliscus*. The close association of the lizards with certain spots along the shore suggests that further study during the breeding season might give some critical evidence on this point.

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SOME VEGETATIONAL RESPONSES AFTER EIGHT YEARS OF PROTECTION FROM GRAZING

In 1934, two pairs of plots were established at the Navajo Experiment Station in northwestern New Mexico for the purpose of observing the effects of protection from grazing on the prevalence of pingue (*Actinea richardsoni* (Hooker) Kuntze). The areas, which at that time were badly overgrazed, were selected because they were heavily infested with this range weed. The sites are nearly level and are in openings in a ponderosa pine (*Pinus ponderosa*) type at an elevation of 8300 feet. The annual precipitation, based on eight years of measurement, is about 17 inches. Table I gives a summary of conditions in each plot. Plots 1 and 3 are fenced. Plots 2 and 4 are unfenced and grazed during the summer months.

The plots are 130 ft. by 65 ft. The original data from each plot, taken in the late summer of 1934, comprised frequency indices from 100, 1 sq. m. and 100, 0.1 sq. m. quadrats taken simultaneously, the smaller frame being set in one corner of the larger. Similar determinations were made in the summer of 1942. Twenty lines of approximately equally spaced quadrats were tallied in each plot.

McGinnies ('34), a part of whose work was done in similar vegetation, demonstrated a high degree of correlation between frequency, as expressed by the frequency index, and abundance. It is apparent from the frequency indices given in table II that, with a few exceptions (notably

TABLE I. *Summary of plot conditions*

Plot no.	Grazing intensities*		Class of livestock	
	Before 1934	Since 1934	Before 1934	Since 1934
1	heavy	none	sheep 85% horses and cattle 15%	none
2	heavy	light	sheep 85% horses and cattle 15%	sheep 80% cattle 20%
3	heavy	none	sheep 85% horses and cattle 15%	none
4	heavy	heavy	sheep 85% horses and cattle 15%	sheep 85% horses and cattle 15%

* "Proper" grazing on the areas is approximately one sheep to 35 acres, year long.

TABLE II. *Frequency indices* *

Species	Plot 1 ungrazed				Plot 2 lightly grazed				Plot 3 ungrazed				Plot 4 heavily grazed			
	1934		1942		1934		1942		1934		1942		1934		1942	
	1 m.²	.1 m.²	1 m.²	.1 m.²	1 m.²	.1 m.²	1 m.²	.1 m.²	1 m.²	.1 m.²	1 m.²	.1 m.²	1 m.²	.1 m.²	1 m.²	.1 m.²
Actinea richardsoni	100	91	53	17	100	83	84	30	99	90	85	26	99	94	99	73
Erigeron flagellaris	74	43	85	69	88	53	92	74	88	65	94	86	64	38	86	78
Agropyron smithii									59	29	73	61	68	35	91	71
Polygonum sawatchense	69	36	3	0	82	54	15	3	55	25	9	3	35	14	59	26
Plantago purshii	49	15	27	13	79	43	54	21	71	38	48	31	47	13	66	35
Sporobolus cryptandrus	38	7	3	1	54	21	4	0	19	2	1	0	18	6	5	2
Chrysopsis villosa	38	7	86	52	38	9	80	47	65	21	90	72	38	15	57	29
Sitanion hystrix	36	8	51	19	31	7	94	46	2	1	52	21	18	6	56	21
Bouteloua gracilis	29	16	33	8	22	12	19	9	17	12	21	9	60	29	68	31
Allium cernuum	16	0	1	0												
Gilia multiflora	14	2	42	11	2	0	14	5								
Lupinus aduncus	10	3	96	62	27	4	91	68	3	0	9	0				
Pentstemon jamesii	9	1	29	10	41	10	65	33	0	0	28	10	6	0	9	2
Astragalus humistratus	7	2	8	1	4	0	5	1	6	1	39	13	11	0	3	0
Thlaspi fendleri	6	0	0	0	4	1	16	8	7	2	11	5	0	0	30	16
Artemisia wrightii	5	0	14	4	9	0	23	7	8	2	20	10	13	2	4	0
Festuca arizonica	4	0	11	3					2	0	1	0	0	0	3	0
Orthocarpus purpureo-albus	4	0	34	5	4	0	20	1	0	0	9	1	0	0	3	0
Koeleria cristata	2	0	8	3	3	1	17	4	0	0	1	0	0	0	5	3
Muhlenbergia montana	2	0	6	0	14	5	18	7	1	1	0	0	2	0	1	0
Allionia pilosa									23	4	6	0	42	26	10	2
Bahia dissecta	0	0	11	1	0	0	1	0								
Carex eleocharis					0	0	1	0	10	3	11	4	5	1	9	6
Erigeron divergens	0	0	4	1	0	0	14	1	0	0	10	2	0	0	21	4
Erigonum alatum	0	0	32	11	1	0	12	7	0	0	28	7	1	0	4	0
Hymenopappus filifolius	0	0	11	2	2	0	9	4					1	0	0	0
Lupinus kingii	0	0	1	0					0	0	21	5				
Oenothera albicaulis					0	0	3	0					0	0	23	10
Pseudocymopteris montanus	0	0	4	0	2	0	4	2	2	0	4	1	16	7	16	5
Senecio neomexicanus	0	0	2	0	1	0	18	6	0	0	8	3	0	0	2	1

* Twenty-five species having indices of less than 10 are omitted.

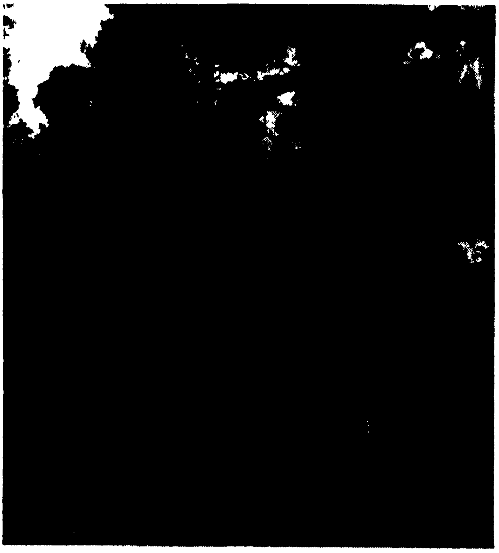

FIG. 1. Plot 3, protected from grazing for 8 years. Note young pines.

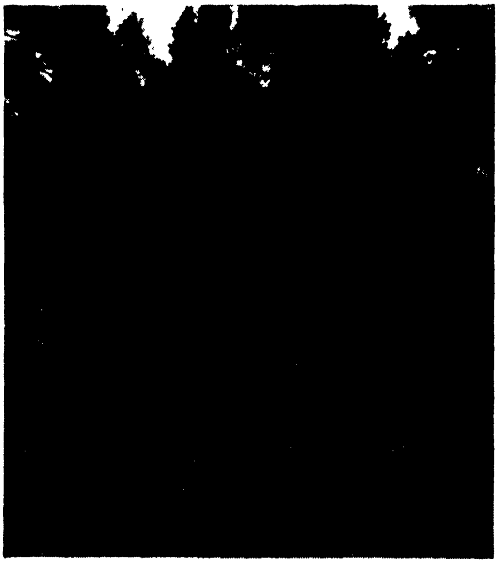

FIG. 2. Plot 4, open to heavy grazing. Note young pines by the stakes. They are of the same age as those in figure 1.

Agropyron smithii and *Sitanion hystrix*), there has been comparatively little change in the vegetation of the heavily grazed plot (plot 4). Pingue may have decreased slightly, as is indicated by the somewhat smaller 1942 index shown by the 0.1 sq. m. quadrats. In plots 1, 2, and 3, on the other hand, pingue had markedly decreased, while such species as *Chrysopsis villosa, Lupinus aduncus,* and *Pentstemon jamesii* had greatly increased. Among the grasses *Sporobolus cryptandrus* had deceased, *Sitanion hystrix* increased, and *Bouteloua gracilis* remained about the same in all plots. Twenty-five species with no index of over 9 per cent have been omitted from the table. Of these minor species, 13 were new in 1942; five had increased and five had disappeared since 1934; and one had decreased and one remained unchanged.

The increase of *Sitanion hystrix* and *Agropyron smithii,* noted even in the heavily grazed plot, may have been due to the two wet years immediately preceding 1942: 1940 was relatively wet, with 19.83 inches of precipitation, while the precipitation in 1941, which was the wettest on record in New Mexico, was 25.66 inches. During these two years both species increased wherever observed on the Station area.

A few qualitative observations in 1942 of the response of young ponderosa pines are worth recording: In plots 3 and 4, there were several small trees—eighteen in plot 3 and twenty-four in plot 4—which ring counts showed to be from eight to ten years old. Those in plot 3 (the protected plot) were from 2 to 3.5 feet tall, with straight stems (figure 1); those in the heavily grazed plot were from 6 to 9 inches tall and had very bushy crowns (figure 2). Very few young pines were found in plots 1 and 2—three in plot 1 and two in plot 2; but the trees in plot 2 (the grazed plot) were as tall and straight as those in plot 1.

The frequency data indicate that partial or complete protection from livestock for eight years has been detrimental to pingue and favorable to the development of several other perennial forbs. It seems that the range, as represented by plots 1, 2, and 3, is still in the early stages of recovery, and there has been no observable difference in the recovery of the lightly grazed area and those receiving complete protection.

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McGinnies, W. G. 1934. The relation between frequency index and abundance as applied to plant populations in a semi-arid region. Ecology **15**: 263–282.

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BOOK REVIEWS

Zoögeography of Tree Snails [1]

Although Darwin first called attention to the part played by isolation in the evolution of new species, it was not until his disciple Romanes had emphasized this principle that it came into prominence. And Romanes based his conclusions largely on the observations of Gulick on the distribution of Achatinellidae in the Hawaiian Islands.

This archipelago is an ideal locality for the study of isolation. Its islands are of volcanic origin, many of them with central craters from which lava ridges run to the sea, radiating like the spokes of a wheel, and dividing the island up into valleys that do not communicate with each other. Physically, the hardened lava does not support vegetation, but it is potentially rich in certain chemicals, which are leached out by the tropical rainstorms and deposited in the valleys, enriching the soil so that it supports dense forests where it has not been disturbed, and extensive pineapple plantations wherever it has been brought under cultivation.

In the tropical forests the birds, insects, and larger animals are able to migrate across the lava ridges but the mollusca are fettered to the soil and it is to them that we must look for light on the problem of isolation.

It is a happy coincidence that the Achatinellidae which are found no where else in the world, should occur in such profusion on these islands. There are several hundred species of these snails, whose shells are so popular with lei makers on account of their great beauty of form and color, and with students of evolution on account of their variegated designs and variability of their band patterns.

In these investigations Dr. Welch has studied over 27,000 specimens of two species of *Achatinella* from Oahu. On each specimen three measurements were made—the elevation of the spire above the end of the suture, the total height of the shell from the apex to the most remote point of the aperture, and the greatest diameter of the body whorl. Unfortunately, his published statistics cover only the height of the shells, and as the probable errors are not shown it is impossible for the skeptical reader to satisfy himself as to the reliability of Dr. Welch's conclusions.

Very briefly, the most important of these conclusions are as follows:

For *Achatinella mustelina*

There are many significant differences in size, color, and shape among series of shells from different localities.

There are no significant differences between series from the same locality, even if taken as many as twenty years apart. This is quite contrary to the conclusion reached by Crampton in his study of *Partula* from Moorea.

There is a significant positive association of ventricosity of the shells with the altitude at which they were taken.

There is no association between the size of the shells and the altitude.

There is significant negative correlation between the size of the shells and intensity of precipitation. This again is inconsistent with Crampton's findings among the Moorea Partulidae. Also, Dr. Welch finds a significant positive correlation between shell size and temperature.

For *Achatinella apexfulva*

There is so much variation in size, form, and color within each locality that it is impossible to tell whether significant differences exist between shells from two different localities unless a very large series is available from each.

There are correlations with precipitation and temperature which appear to be the reverse of those observed for *Achatinella mustelina.*

No significant difference in size can be observed among series from the same locality over a period of years.

The correlations of shape with altitude, and those of size with precipitation and temperature, are interesting, but would have been more impressive had the coefficients been published. The reason for their omission is obvious. Dr. Welch did not collect these shells himself, but had to be satisfied with what he could find in museums. Many of the series did not contain sufficient specimens to justify computing correlations or probable errors. And when a series is large there is frequently no way of knowing whether the original collector deposited his entire catch, or whether the curator may not have used some of the specimens in exchanges. If, in the latter case, he exercised any freedom of selection, the remaining series would not be representative. Dr. Welch has done an excellent piece of work with the material available, but unfortunately museum material is not ideal for quantitative investigations.

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[1] **Welch, D'Alte.** 1938. Distribution and variation of *Achatinella mustelina* Mighels in the Waianae Mountains, Oahu. Bernice P. Bishop Museum Bulletin 152.

Welch, D'Alte. 1942. Distribution and variation of the Hawaiian tree snail *Achatinella apexfulva* Dixon in the Koolau Range, Oahu. Smithsonian Miscellaneous Collections. Volume 103. No. 1.

Both of these species exhibit one peculiar trait—the shell may be indifferently dextral or sinistral. Perhaps the most striking feature of this investigation is the proportion between the numbers of dextral and sinistral specimens from a single locality. In a stable population in which dimorphism based on a single Mendelian factor occurs, and where random mating takes place, the number of impure dominants is equal to twice the square root of the product of the pure dominants by the recessives. But Gulick's observations led him to believe that heterostrophic copulation could not occur, and that consequently mating could not be random. If Gulick's supposition is correct, no mixed population can be stable, for with each successive generation the disparity in population between the two forms will increase and stability will be achieved only with the disappearance of one form.

Under such circumstances we should expect to find very few localities in which dextral and sinistral shells occurred in approximately equal numbers, but many in which one form (it matters not which) prevails with the other represented by only a few sporadic individuals. Reference to Dr. Welch's statistical tables reveals that the shells occur in exactly this distribution, a fact which seems to lend considerable support to Gulick's theory.

The only adverse criticism that can be made of these investigations is the paucity of the writer's bibliography, the combined lists of references affording only a dozen titles. Surely there are other studies of geographic distribution that might profitably be compared or contrasted with these.

Both reports are well illustrated with photographic plates, but black and white are completely inadequate to do justice to the brilliant coloring of the shells.

Joshua L. Baily, Jr.

Systematics and Speciation [1]

Those biologists who view taxonomy as a dull process of attaching names to specimens would do well to read the recent books by Dobzhansky, Huxley and this new work by Mayr. Mayr probably handles zoögeographical problems in relation to speciation and raciation more comprehensively than any other author. The emphasis is naturally upon birds because of the author's research interests. However, illustrative examples from other groups are given also. The rôle of taxonomy in the analysis of evolutionary factors is the main contribution of the study, but these relationships are discussed from the broad perspective of genetics, physiology, behavior and ecology.

The book is of particular interest to ecologists who are interested in evolution, zoögeography and faunal distribution. Zoögeographical isolation receives the primary consideration while ecological, seasonal, psychological and sexual isolation are relegated to subsidiary importance and deemed the secondary effects of geographical isolation in the large majority of cases. The topics of special ecological interest include temperature tolerance and preference, sex and reproduction, sexual dimorphism, habits and life history, migration, habitat preference, phenotypical changes, polymorphism, adaptive variation, ecological rules such as Bergmann's rule and others, clines, population structure and variation, double invasions, ecological races, and ecological barriers.

Were it not for the fact that reviews in this journal are traditionally critical, I should not be inclined to pick out the weaknesses for fear of disproportional accentuation. Most of the errors are those of omission. For instance, physiological experiments on species distinctions such as those studied by M. R. Irwin and L. J. Cole are left out. Also bird speciation gives a more adequate picture of the evolution of behavior through nest building activities and courtship than could be found in almost any other group, but such data are not analyzed. Mayr interestingly separates the term "ecological" from "ethological" which refers to behavioristic factors.

Errors of commission are more difficult to find and in each case there might be quite valid argument as to whether the critic or the author were in the right.

Mayr includes within the species definition those populations which are potentially capable of interbreeding even though they may be wholly isolated by means of geographic barriers. Thus his concept of the species is broader than those of us who would make a separation when genetically distinctive natural populations were reproductively isolated even though potentially still able to interbreed if brought into contact. Both demarcation lines are of prime importance in evolution. However, the reviewer is of the opinion that isolation, regardless of type, has similar evolutionary consequences in the majority of cases while Mayr emphasizes the permanent separation of populations through sexual, physiological or behavioristic incompatability. I should think that the lack of interbreeding would be easier to determine for practical taxonomy than would the potential inability to interbreed in separated groups, but Mayr seems to be convinced to the contrary.

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[1] **Mayr, Ernst.** 1942. Systematics and the origin of species. New York: Columbia Univ. Press. xiv + 334 pp. 29 figs. $4.00.

A taxonomist dealing with large organisms with unusually good means of locomotion would be likely to find that geographical isolation together with broad ecological differences in geographical habitats outweigh other factors in giving the best phylogenetic correlations. Although Mayr analyzes many cases of sympatric species, I am inclined to believe that a student of speciation of parasites or of organisms confined to single species of food plants might be able to correlate his phylogenies better with ecological factors than with geographical causes. However, it is necessary for ecologists to study many cases carefully before it is possible to refute Mayr's contention that geographical and not ecological isolation is primary in nearly all instances.

The book is particularly valuable in reviewing much European literature and in tabulating data from a quantitative viewpoint. Many special illustrative cases are compared for the first time. The work is a thoroughly scholarly treatment of a growing field of interest to ecologists.

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TESTAMENT OF A NATURALIST [1]

That the more consciously scientific ecology has grown out of the less critical natural history of earlier generations has become something of a commonplace observation. It must be maintained that there were in fact critical and reflective naturalists long before the rise of modern ecology. The terms "naturalist" and "ecologist," in spite of their broad overlap, still involve useful distinctions; it is evident that Joseph Grinnell thought of himself as a naturalist, for the word "ecology" appears in the collection of his essays here reviewed only in the occasional adjective "ecologic."

Joseph Grinnell played a leading part for a generation in maintaining the values of "natural history" in a university world in which the experimental method was worshipped in the shrine of the laboratory. He called attention to the age-old experiments of evolution to be observed in nature, and insisted upon the value, both relative and intrinsic, of the fact gathering of the field naturalist. He was himself a specialist in the systematics of birds and mammals. From this vantage ground he studied the geography of the species and subspecies, the factors limiting their distribution, and the kinds of variation reflected in these categories. Much of his attention came to be directed to more strictly ecological interests, especially to the examination of population trends in nature, to the agency in soil formation of burrowing rodents, and to the broad field of conservation. His most notable published volumes are on the vertical and areal distributions exhibited in the rich fauna of California. In them he appears as a thinking naturalist, thinking about the implications, the meaning, and the origin, of the phenomena under consideration.

Reviewing Grinnell's career in the light of the essays and extracts now gathered into book form, his importance as an organizer and director of a research museum is appreciated. Only a strong character and an enthusiast could have established a museum in one of the greatest universities, and maintained the prestige of his research students at the very time when a famous geneticist had scolded museum zoölogists as being no better than postage stamp collectors. Three essays on the functions and conduct of a research museum reflect the growth and something of the spirit of the Museum of Vertebrate Zoölogy at the University of California, of which Grinnell became director in 1908. One of these, "The Museum Conscience," fell into my own hands at the beginning of my career at Field Museum, and profoundly affected my attitude toward my work and toward the organization of which I became a part; it impressed upon me that museum routine could neither be despised, neglected, nor delegated; and it gave me faith that consciencious attention to the factual data that accumulate in museums would not only make me a curator in the best sense, but might earn for me the title of "naturalist."

Grinnell had the intention of unifying his lifetime observation of the phenomena of animal distribution into a book; his premature death—he was young at 62 when he died—robbed us of a superlative worker in this field. Biologists in general should be the more grateful to the editor for the excellent selections from Joseph Grinnell's published work, and in the fine format of the book the University of California compliments itself as well as its distinguished teacher-naturalist.

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[1] **Miller, Alden H.** (editor). Joseph Grinnell's philosophy of nature. Selected writings of a western naturalist. Berkeley and Los Angeles: University of California Press. Pp. xv + 237, 13 illus. (3 in color). $2.00.

Ducks, Geese and Swans[1]

In order to justify the publication of a new book on ducks, geese and swans the author must be able to contribute new material or bring together data which have not been easily accessible to the average reader or present existing information in a form that constitutes a definite addition to the literature on the subject. Mr. Kortright has fulfilled the latter two of these three requirements in an admirable manner. The book begins with a general description of the family Anatidae (ducks, geese, and swans) including a chart of the subfamilies, genera, species and subspecies. Then come number of chapters including duck topography and anatomy, identification of specimens, age and sex determinations, mating, nesting and feeding habits, longevity records, speed of flight, migration routes and fly ways, banding water fowl, etc. This section contains a great deal of diverse but cogent data brought together from various sources and presented in an unusually readable form. The main part of the volume consisting of the description, identification and life story of each species combines an orderly arrangement of facts with an interesting account of the natural history. The author has drawn from a wide range of writers, naturalists, ecologists, and sportsmen for the life stories. Many of the quotations from such authors as Audubon, Bent, Elliott and others are of a high order of literary merit. Accompanying the description of each species is a small map of North America showing their breeding grounds and winter habitat. The seasonal migration of these wild fowl, to which considerable space is devoted, has a certain romantic appeal to most of us. This is perhaps due to our envy of the bird's capacity to fulfill its desires not only in escape from the rigors of extreme temperatures but also in finding regions of isolation and security such as are afforded by the arctic tundras where the swans, geese and ducks build their nests.

The book contains a good deal of information of an ecological nature scattered through the life stories of the different birds. However, the only data of this kind which are systematically presented are those on the stomach contents. The illustrations are copius and excellent, particularly the thirty-six color plates at the end of the volume. These colored illustrations depicting practically all the birds described in the text, include' both the winter and autumn moult plumages, the latter constituting a distinct aid to the identification of the species. There are also several plates of the downy young and hybrids. Ducks, Geese and Swans should interest a wide range of readers from the serious student of this branch of ornithology and bird behavior to the sportsman and the individual who appreciates first rate accounts of wild life.

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Sampling Methods in Forestry[2]

This bulletin, outlining sampling procedures for practical forestry problems, should be helpful not only to the practicing forester but to anyone confronted with the problem of sampling plant or animal communities.

The authors have certainly performed a good service by assembling in one place the essence of a large part of the widely scattered literature on sampling and organizing it into an exposition having logical continuity. Their alleged purpose in so doing is to acquaint the practicing forester with the art of planning and executing suitable sampling procedures so that a valid estimate of sampling error can be calculated and so that the real error of the average will be as small as possible consistent with allowable time and funds.

Probably foremost among the features that make this bulletin of particular value to the ecologist is that it deals with sampling problems especially familiar to him. Sampling complex communities where two to many species occupy the same site; sampling attributes that are often difficult and time-consuming to measure; and sampling types that are typically of irregular outline and unknown area are problems with which the ecologist is often confronted. Methods appropriate to these special problems are discussed in this bulletin and illustrated using data largely drawn from forestry.

But unhappily the discussion of procedures is neither simple nor easily understood. True, the first chapter treats with the simplest basic conceptions of sampling, which an elementary reader can easily comprehend. But this brief discussion of fundamentals would not enable the reader easily to understand the more complex discussions that follow unless he already possessed a reasonable knowledge of statistics. The non-mathematical reader is further handicapped by the very frequent use of equations in developing the discussions. There is much valuable material in the bulletin that would be used by a large body of the foresters, range technicians and ecologists if it were more clearly expressed.

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[1] **Kortright, Francis H.** 1943. The Ducks, Geese and Swans of North America. Washington, D. C. The American Wild Life Institute. Pp. 476. $4.50.

[2] **Schumacher, F. S., and R. A. Chapman.** 1942. Sampling methods in forestry and range management. Duke University School of Forestry Bull. 7, 213 pp., 26 figs., 50 tables. Durham, North Carolina, $2.00 (paper)—$2.50 (cloth).

The emphasis throughout this bulletin is on the need for random sampling and this is entirely appropriate in experimental types of work where the need for an unbiased estimate of error is clearly of primary importance. Indeed, this is the situation most often faced by the ecologist. But sometimes in practical ecological work, as in the resource survey type of sampling, accuracy in the estimate of the population average is of greater importance than validity in the estimate of sampling error. In such cases, systematic sampling, leaving out all considerations of convenience, is the better choice because it generally provides a more accurate average than is given by random sampling of equal intensity. The estimate of sampling error of such systematic surveys is unquestionably biased when calculated by methods appropriate only to random sampling, but it does furnish information of some value. It is of interest in this respect to note that there is now available an apparently valid method whereby an unbiased estimate of error can be calculated from data furnished by systematic sampling.[2] By and large, the decision on whether to sample systematically or randomly is not always in favor of random, as the authors of this bulletin would have the reader believe.

Considering all aspects, the virtues of this bulletin more than outweigh its faults. It is a useful text on sampling for the ecologist as well as the practicing forester, more so to those with a fair knowledge of statistical techniques than to the elementary student.

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[2] **Osborne, James G.** Sampling errors of systematic and random surveys of cover-type areas. Jour. Amer. Stat. Assoc. **37**: 256–264. 1942.

RANGE MANAGEMENT[1]

For many years there has not been an up-to-date and comprehensive treatise of range management. In the meantime, there have been important developments which too often were not adequately covered in the literature or were so scattered that only specialists were aware of their existence. Stoddart and Smith have attempted to rectify this situation by writing the most comprehensive treatise on range management that has so far been developed.

In the first chapter, the authors define range management as the science and art of planning and directing range use so as to obtain the maximum livestock production consistent with conservation of the range resources. Then they proceed to cover the art and science of range management in a very comprehensive manner. The 514 pages of text material are packed with information. Each of the 20 chapters covers a separate phase, which gives some idea of the wide scope and many ramifications of this subject. The first four chapters are devoted to history and to a discussion of the place of the range industry in the modern world. The next two chapters are devoted to plant ecology and physiology, covering grazing regions and the reactions of individual plants to their environment and to grazing use. Chapters 7–12 cover such technical phases of range management as nutrition, range surveys, range management, and range animal husbandry. In the succeeding chapters, range development, artificial seeding, effects of burning, soil and water conservation, and poisonous plants are considered in turn. The important, but often neglected, subject of native fauna in relation to grazing use is discussed in chapter 18. The last two chapters are devoted to range economics and administration of public lands.

Bringing all of this information together in one book represents a major task. The literature coverage is adequate; in fact, it may be that the authors have attempted to bring in too much at the expense of too little attention to some of the more important developments in the field of range management.

The authors do not clearly indicate the specific purpose for which the book is intended, but it appears to the reviewer that they have attempted to develop a text of universal use; one that would serve for an introductory course in range management or that could be used by students of forestry and animal husbandry who have only a small interest in range management, and a book that could be used by practical stockmen and workers in the general field of range management. They have succeeded in developing a text of broad use, but by so doing they have somewhat decreased its value for instructional purposes. The treatment of certain fundamental phases of range management, such as ecology, surveys and management, is too brief to suffice the needs of the specialized student. On the other hand, the rather full discussion of some of the controversial problems in the field will probably be confusing to those having only a minor interest in the subject.

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[1] **Stoddart, Laurence A., and Arthur D. Smith.** 1943. Range management. New York and London: McGraw-Hill Book Company, Inc. xii + 547 pp. 165 figs. $5.00.

The beginner is apt to be somewhat confused by the introduction of material bringing out various angles but which may be more or less contradictory. There are many examples, but two will serve to illustrate. On page 204, the authors state, "The species list . . . is not a good quantitative method." In the same paragraph and referring to the same method, it is stated, ". . . the distribution or frequency of occurrence of each species can be determined with great accuracy." While the advanced student may see no inconsistencies in these statements, they may be confusing to the neophyte who does not recognize the difference between quantitative and qualitative studies. On page 219 in referring to the use of aerial maps and contact prints for surveys, it is stated, "The mosaic is only slightly more free from error than the contact prints," and on page 221, "Field mapping may be done directly upon the mosaic, though the resultant map is likely to be less accurate than that from contact prints." Probably less of the usual pressure to hurry up publication would have afforded opportunity to eliminate such minor inconsistencies.

The ecologist may be disappointed in the treatment given "grazing regions of the west." The authors have developed their own map and this, together with descriptions of the vegetation to be found in various regions, will no doubt bring forth expressions of differences of opinion by local ecologists. For example, the California ecologist may reluctantly admit the existence of an "arm" of the California chaparral in Arizona; but including the oak thickets of Colorado and the shinnery oak of New Mexico under the term *chaparral* will not meet with general approval among southwestern ecologists.

The map on page 67, showing natural vegetation of the range states, does not add credit to the book. The legend is too small to be deciphered easily and the spelling of *piñon* is disconcerting, to say the least. Close examination by use of a hand lens shows a discrepancy between legend and map. In the legend, bunch grass is indicated by means of parallel lines of small circles, while on the map it is shown by alternating dots and dashes.

Making due allowances for small-scale map inaccuracies, it would still be hard to convince a local resident that the extent of bunch grass along the southern boundary of California is shown properly. On the other hand, desert grassland has been slighted in southeastern New Mexico.

While the illustrations are generally good, the maps prepared by the authors are below the high standards of the remainder of the material. The legend is almost undecipherable by the naked eye (figures 1 and 11) and hatching is unevenly done.

The authors are to be commended in bringing together such a wide variety of material. They have not neglected any of the related subjects of major importance. While in a strict sense they may have invaded the fields of animal husbandry, economics and conservation, all of these are closely interrelated with range management, and an understanding of their relation is fundamental to successful range practices.

The book is easily read; the type is clear with few typographical errors. Arrangement of the material is excellent. The index shows considerable thought in preparation and should be extremely useful to those using the book for reference purposes.

Terminology is generally consistent with common usage, but the dyed-in-the-wool range manager has not accepted the term *forb* and still looks on it as a sissy substitute for *weed*. The author's adherence to the term *carrying* capacity is rather surprising, as *grazing* capacity has become widely accepted even among stockmen.

As a general reference book for those working in related fields, it is highly recommended. It is also recommended as a text for general courses in range management. When used in conjunction with lectures, field and laboratory work, it should also serve as a satisfactory text for students majoring in the field of range management.

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Los Angeles, California

Elton, Charles. 1942. Voles, mice and lemmings; problems in population dynamics. Oxford: The Clarendon Press. Pp. 496, 22 figs., 67 tables. $10.00. Although writing in what might be regarded as semi-popular style, Elton presents subject matter of very complex nature. His evident intention is to bring together the existing knowledge on fluctuations of mouse-like rodents and related phenomena, a task for which his qualifications are virtually unique. Few actual conclusions as to causes of violently cyclic fluctuations are given, but the dissertation is rich in evidence, all of which strengthens the scientific standing of the book; real understanding of some, or conceivably most, of the factors discussed may be too much to expect for any years to come, but contemporary students should find this work of outstanding value as a reference, from which they may at least partially appraise contributions of the past and gain familiarity with trends revealed by the data. Part I, pertaining to vole and mouse "plagues," contains a great deal of historical information, also a most valuable account of ecological researches on rodents in the U. S. S. R. Part II summarizes the British studies with which Elton himself has been associated and includes a chapter on lemming cycles in Scandinavia. In parts III and IV, biological and social ramifications of fur and rodent cycles of northern Labrador and Ungava are portrayed. Bibliographies are terminal to the chapters, and there is an 8-page index.—P. L. E.

Russell, E. S. 1942. The overfishing problem. Cambridge, England: The University Press. Pp. vii + 130. This excellent little book by the distinguished English biologist, E. S. Russell reproduces the DeLamar lectures given at the Johns Hopkins University in 1939. The book successfully applies certain principles of population ecology to an economic problem—the effect of ocean fishing on fish stocks and the powers of regeneration of these stocks in the face of such pressure. There were five lectures in all and they form the following five chapters: "The exploitation of the fish stocks"; "The depletion of the older grounds"; "Age analysis of fish populations, mortality rates and rate of growth"; The overfishing problem in its modern formulation," and "The regulation of the sea fisheries."

The author draws the following "main conclusion": "We are justified I think in drawing the general conclusion that, with the exception, at the present time, of the cod in the far north—and doubtfully in Iceland—the principal species of demersal [bottom] fish sought for by British trawlers are being definitely overfished, in the sense that the intensity of fishing has gone beyond the optimum and has resulted in depressing stocks below their most profitable level."

This book should be read by every ecologist!—T. P.

Hamilton, W. J. (Jr.). 1943. The mammals of Eastern United States. Ithaca, N. Y.: Comstock Publishing Company. Pp. 432. With thirty animal portraits by Earl L. Poole. $4.00. Doctor Hamilton is placing ecologists, mammalogists and systematists increasingly in his debt by his general publications on mammalogy. First there was his well-received book "American mammals" and now "The mammals of Eastern United States." The present book ". . . is intended to give brief descriptions and accounts of the distribution and habits of all the present day land mammals naturally inhabiting the states east of the Mississippi River. It is designed for students of mammalogy and for the increasing number of laymen who are interested in this important aspect of wild life."

The material follows a taxonomic organization with a chapter for each major group as follows: Marsupialia; Insectivora; Chiroptera; Carnivora; Rodentia; Lagomorpha (hares and rabbits); Artiodactyla, and Xenarthra (edentates). For each group an identification key is given which takes the specimens to genus. Then the species are considered one-by-one. The data typically discussed here are description or appearance, distribution and habits. This treatment is embellished by frequent photographs and "animal portraits" as well as by excellent distribution maps. There is a first-rate bibliography and an adequate index.—T. P.

Adolph, Edward F. 1943. Physiological regulations. Lancaster, Penna.: The Jaques Cattell Press. Pp. xvi + 502. $7.50. The contents of this book are abstracted by the author as follows:

"This is a monograph recording an investigation in quantitative physiology. Regulations in organisms are maintenances of relative constancies. They are described from suitable data by selected relations of the following sorts:

(1) Variations, especially in the successive values found for one sort of measurement in an individual. These represent the results of all those events that antagonize the occurrence of wider variations.

(2) Changes and exchanges as correlated with excesses over, or deficits under, the control values (contents). These are rates of processes, and express what is done to recover the usual physiological state.

(3) Behaviors that exhibit preferences for

environments which either promote or prevent exchanges of diverse components.

Water is chosen as the prototype of component that tends to be in quantitatively regular amounts in living units. . . . Analogous data are set forth concerning other quantities than water. Some of these are heat, glucose, oxygen, carbon dioxide, lactate, frequency of heart beat, and blood pressure. For each a similar pattern of equilibration is found."

The text is divided into two major sections: water relations of animals, and regulations of several components and in general. The treatment is comparative for, although the dog is stressed, there are data on man, frogs, rabbits, snakes, mollusks, annelids, insects, echinoderms, etc.

The value of this volume for ecology is considerable. There is much in autecology that finds emphasis here. The modern ecologist is interested in this "larger physiology" and, in particular, in the regulatory abilities of the total organism. In fact, the central theme of this book—"what do animals do to maintain their physiological constitutions and activities"?—is basic in understanding the organism and its relations to the external environment.

We commend this book. It is both unusual and thought-provoking.—T. P.

Dahlberg, Gunnar. 1942. Race reason and rubbish. A primer of race biology. New York: Columbia University Press. Pp. 240. $2.25. This volume has been translated from the Swedish by Lancelot Hogben who has this interesting comment to make in the Foreword: "This book deals with biological aspects of the race problem, and the Scandinavian antecedents of the author give a peculiar piquancy to what he has to say about the suppositious superiority of the Nordic Man. Professor Dahlberg is one of the six living people [it would be entertaining to learn the names of the other five] who know most about heredity. He is unique in bringing to his work the severe discipline of Swedish medical education, a sound grasp of statistical method, humane judgment and horse sense. As head of the State Institute of Race Biology and, at the time of writing, Dean of the Medical Faculty in the University of Upsala, he is recognised as the leading authority on Human Genetics and Medical Statistics in the Scandinavian countries."

The book is a brief review of the mechanism of heredity (chapters 1–4); of certain aspects of physiological genetics (chapter 5); of the statistical concepts of random mating and selection (chapters 6 and 7), and, finally, of certain population aspects of human genetics; e.g., inbreeding and cousin marriage, assortative mating, the isolate effect, race and the Jewish question. The author's major focus seems to be to give the reader an evaluation of racial problems through the portal of sound genetic principles.

Storer, Tracy I. 1943. General zoology. N. Y.: McGraw-Hill Book Co., Inc. Pp. xii + 798. $3.75. "This text provides a general introduction to zoology, primarily for students in colleges and universities. It comprises a general account of animal biology and a systematic survey of the animal kingdom from protozoans to man." The book starts with discussions of "principles." These are followed by a treatment of the major animal groups in ascending complexity. A number of new summary tables and illustrations enhance the book's worth. The format, style and workmanship are first-class and there is a good index and a carefully selected bibliography. The treatment of phylogeny is not strong.

MacDougall, Mary Stuart. In collaboration with **Robert Hegner.** 1943. Biology the science of life. N. Y.: McGraw-Hill Book Co., Inc. Pp. x + 963. In this volume the authors have strived for a presentation that will permit the biology instructor to follow his own ideas of organization. This is accomplished by arranging the material in major sections which can be assorted independently of each other. This seems a good idea. The sections are "The foundations of biology"; "Plant biology"; "Animal biology"; "General biology: organs, systems, and their functions; the biology of man"; "Some biological principles and theories"; "Applied biology; biology and human welfare; conservation," and, "The history of biology." In the index (which is a good one) there appear two page references to ecology both of which are essentially definitions and a brief discussion of the environment under "adaptation." Also in an appendix there is a "synopsis of communities" adopted by the Ecological Society of America. Genetics, on the other hand, is represented by 44 items under that heading in the index. The physical make-up of the book is excellent. The bibliography and glossary are usable.

Rush, William M. 1942. Wildlife of Idaho. Boise, Idaho: Fish and Game Commission. Pp. 1–299. 14 colored plates, 74 photographs and 1 drawing. $1.00. This book was prepared for the public schools of Idaho and presented to them by the Idaho State Fish and Game Commission. The Commission realized that to effectively administer the wildlife resource they must have the support of an intelligent public opinion.

The author has acquired his knowledge of these animals by contact in the field extending over a period of more than a quarter of a century. For 22 years he was a ranger in the Forest Service, giving his attention almost entirely to game problems on which he is widely recognized as an authority. In this book he has had assistance from schoolmen in order better to adapt it to the needs of grade school children. Much of the subject matter is first-hand and in this respect is material worthy of consideration by even those who are carrying on research in this field.

The book follows the conventional division into three parts: one on Mammals, one on Birds, and one on Fishes, of 150, 59 and 64 pages, respectively. The introduction distinguishes briefly the difference in the animal, plant and mineral kingdoms, and in mammals, birds, fishes, amphibians and reptiles. In the classification of mammals, technical terms are avoided insofar as possible, but the idea and need of a classification simply stated.

The discussion opened with the meat-eaters, beginning with the dog family. The approach is general, one might almost say ecological, since much of the history and environment and interrelation of the animal to man and other animals is woven into the discussion. There is little or nothing of morphology or physiology, but a good deal of history and ecology. The dog family is followed by the cat family. Then follows a unique character of the book, a pioneer story dealing with the early life of the region as affected by the animal under discussion. Here is contained much of the value of the book for child or adult reader. This is followed by the bear family, winter sleep, the weasels, the shrews, the bats and the rodents, and another frontier story, bringing out the life history and uses of the beaver. This method is followed throughout the book.

A notable chapter, Early History in Idaho, brings out the importance of deer to the early settler and is followed by a development of the need for rules in using wildlife so as to prevent its destruction.

It is distinctive chiefly because of the first-hand material it contains, of the popular presentation, and the field it covers. In a real sense it touches the broad field of ecology, chiefly that field dealing with the relation of man to the larger animals about him. Its use should by no means be limited to Idaho since it is almost as applicable to any of the western States and applicable to any region in its broader approaches.

Rush, William Marshall. 1942. Wild animals of the Rockies, adventures of forest ranger. New York and London: Harper and Brothers. I-XXII, Pp. 1-296, 20 photographs. $3.00. The author here records personal experiences with wild animals during a period of 22 years while he served as a ranger in the Forest Service of the U. S. Department of Agriculture. These experiences are recorded in 9 chapters on bears, grizzly and black, 3 chapters on elk, 1 on moose, 5 on deer, 3 on antelope, 2 on buffalo, 8 on mountain sheep, and 3 on mountain goat.

Here is a wealth of information about these animals, including such matters as predation, elk tooth hunters and the social habits of the different animals, and even a mention of diseases and personal combats between males. To those who are interested in the life habits of those animals the book contains valuable first-hand observations.

Conditions since his observations were made have not changed greatly except that deer, elk and moose are now more numerous. A trip over any of the country described is likely to result in contact with the same animals. Descriptions are accurate and non-technical. As reading matter it should attract anyone interested in the out-of-doors and in these animals. The ecologist, plant or animal, will here find first-hand observations, some of which might require years to observe but nonetheless necessary to an understanding of the life habits of these animals. It differs from most books of this type since it is not written from the standpoint of the hunter but from that of the naturalist, interested primarily in the welfare of the animals themselves.

Ladd, Harry S. 1942. Report of the committee on marine ecology as related to paleontology. Division of Geology and Geography, National Research Council. Pp. 58. $0.50. The report for 1941-1942 of the Committee on Marine Ecology as related to Paleontology has recently been issued by the National Research Council. It is a bound mimeographed bulletin of 58 pages, containing material presented last May at the Annual Meeting of the Division of Geology and Geography. It is similar to the report of the Subcommittee on the Ecology of Marine Organisms issued a year ago.

The report gives information on current and recently completed activities together with a current bibliography and summary reviews. Included also are seven signed reports dealing with special ecologic studies. The Division of Geology and Geography believes the report will be found useful by paleontologists. Complimentary copies have been sent to contributors but the Division is unable to distribute such copies as widely as heretofore. Requests for copies should be addressed to the Division of Geology and Geography, National Research Council, 2101 Constitution Avenue, Washington, D. C., accompanied by a remittance of fifty cents for each copy desired.

Wallace, Frederick William. 1942. Canadian fisheries manual. Gardenvale, Quebec: National Business Publications. 1-102 + 1-116 pp., plates, figures. $3.00. A well-illustrated review of the fishes, fishing grounds, methods of capture and preparation for market, and economic importance of the Canadian commercial fisheries, both marine and freshwater. This is a valuable exposition of an industry of great importance in time of war, and was written with a view to providing a source of fisheries information for students and teachers in schools and colleges.—KENNETH H. DOAN, F. T. Stone Laboratory, Ohio State University, Put-In-Bay, Ohio.

Knight, Harry H. 1941. The plant bugs, or Miridae, of Illinois. Bulletin of the Illinois Natural History Survey **22**: 1; 1–234. **Frison, T. H.** 1942. Studies of North American Plecoptera with special reference to the fauna of Illinois. *Ibid.* **22**: 2; 235–355. These two useful monographs are contributions from the Section of Insect Survey of the state of Illinois. They appear to be usable, authoritative, well documented and well illustrated and will be welcomed by the ecologist as further aids to the solution of his taxonomic problems.

ECOLOGY

VOL. 24 OCTOBER, 1943 No. 4

REPLACEMENT OF TRUE PRAIRIE BY MIXED PRAIRIE IN EASTERN NEBRASKA AND KANSAS[1]

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Destruction of a portion of one plant association and its replacement by another has just been completed. This has occurred not as the result of man's interference with the vegetation nor the effect of his grazing animals. It has been due to a dry climatic cyle and has been accomplished within a period of seven years. The scene of action was the broad area on the western edge of true prairie in central Kansas, eastern Nebraska, and eastern South Dakota. It is distinctly east of the mixed prairie in the central portion of these states. Although the phenomenon was general over hundreds of square miles of grassland, it has been studied in detail from year to year in only a few widely separated places. Three of these have been selected to illustrate this remarkable transition in grassland populations and structure and the manner in which it occurred, as well as the time relations and the causal factors.

True prairie is characterized by a continuous stand of certain dominant grasses of medium stature—mid grasses. Although there is an under layer of forbs with a few low-growing grasses, these form open stands, are not continuous, and are distinctly subdominant. Hence, true prairie is readily distinguishable both in physiognomy and structure from mixed prairie with its dominant mid grasses and dominant short grasses. These typically form an upper story and a lower layer respectively, or short grasses of the drier places may alternate with the mid grasses of less xeric sites. In addition, the eudominants of the two associations are, of course, different, and even the perdominants exhibit differences in appearance, in size, and often in habits of growth in the two associations (cf. Clements and Shelford, '39).

SAMPLE PRAIRIES

The three prairies selected for illustration had been studied at two periods just before the drought and intensively summer after summer following 1934. They are located, respectively, 65 miles southwest of Lincoln near Carleton, Nebraska; 30 miles northwest of Carleton near Clay Center, and 45 miles southwest of Carleton near Montrose, Kansas. These bluestem prairies were ungrazed but mowed in fall for the crop of hay. They were entirely representative of the area as a whole, considerable parts of which are still unbroken prairie and pasture land. They are in the Chernozem zonal or climatic soil group.

The Carleton tract is a nearly level upland prairie formerly 80 acres in extent, with a broad shallow ravine running its entire length. The soil is Crete silt loam and, like the following soils, is described by Robertson ('39): "The topsoil is dark brown to black and coarsely granular. Lime is generally present at a depth of 2 to 3 feet and the soil is brown to light brown, hard, and rather impervious at this depth. In the swale in the wheat-grass type a definite claypan is present beginning at 9 to 12 inches and extending to depths of 26 to 30 inches. Over the remainder of the prairie this layer is present but more pervious and less superficial."

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[1] Contribution from the Department of Botany, University of Nebraska, No. 141. This study was made with the aid of a grant from the Penrose Fund of the American Philosophical Society.

The grassland at Clay Center is a well-drained unbroken tract, formerly of about 20 acres, crossed by a shallow swale. The soil is Hastings silt loam. "It is readily penetrable by water and roots and has the lime layer at a depth of over 4 feet. This type is considered excellent for corn and is almost entirely under cultivation in Clay County."

The Montrose prairie consisted of 60 acres of moderately rolling land with some nearly level areas and shallow ravines. "The soil in the ravine is Lincoln silt loam, colluvial phase; that of the slopes is Colby silty clay loam. The 6-inch layer of eroded topsoil is a dark, pervious mantle of silt loam underlain by a subsoil consisting of about 20 inches of grayish to light brown, slightly compacted silty clay loam above unweathered loess."

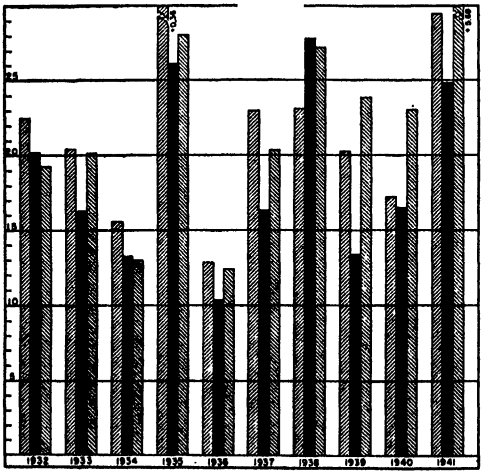


FIG. 1. Annual precipitation in inches near the prairies at Clay Center (black), Carleton (diagonal lines at left), and Montrose (diagonal lines at right) from 1932 to 1941 inclusive.

DROUGHT AND CHANGES IN VEGETATION

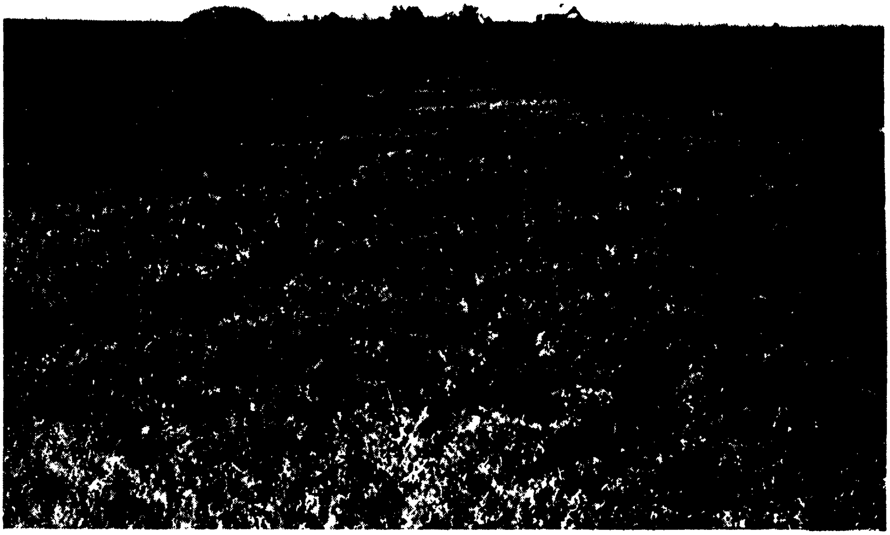
The normal precipitation is 27.3 inches near Carleton, 25.5 at Clay Center, and 25.0 inches near Montrose. Annual precipitation at these stations is given for two predrought years, the extremely dry years of 1934 and 1936, and the remaining years until the drought was definitely broken in 1941–42 (figure 1).

The broad outlines of the changes in the vegetation year by year that resulted in mixed prairie are as follows:

1932–33	Predrought bluestem prairie
1934	Great deterioration
1935	Western wheat grass spread widely
1936–37	Further losses; wheat grass increased
1938	Wheat grass and short grasses increased; revival of relicts
1939	Side-oats grama increased greatly and competed successfully with wheat grass; short grasses increased
1940	Great losses of prairie relicts and side-oats grama; wheat grass and short grasses possessed the prairie
1941	Mixed wheat grass—short grass prairie

The terrific impact of the drought in 1934 has been described (Weaver, Stoddart, and Noll, '35). Likewise the results during the following year (1935) in Iowa, Nebraska, and Kansas have been fully presented (Weaver and Albertson, '36). The results of intensive field work in these and adjacent prairies during 1936 and 1937 have been fully described by Robertson ('39). Further studies on the progress of the recovery of vegetation from drought over a wide area until 1939 have been reported (Weaver and Albertson '39, '40, '40a).

Numerous other researches reveal not only the great intensity of the drought but also the very large area of grassland



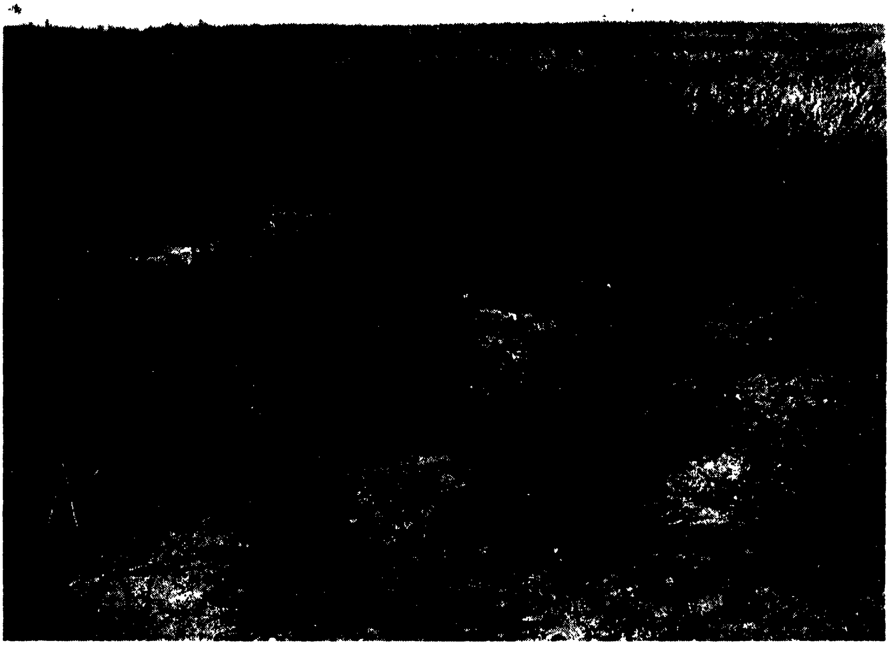


FIG. 2. View in Carleton prairie in spring, 1940. The shallow swale in the foreground (light color) is occupied mostly by relict big bluestem. Western wheat grass (dark color) occupies three-fourths of the prairie. It is 8 inches tall, and extends beyond the haystack for a quarter of a mile. The bluestem area is being invaded by wheat grass.

FIG. 3. Relict bunches of big bluestem that have recovered from burial by 2 to 4 inches of wind-blown soil. They are completely surrounded by western wheat grass which invaded this area and caused dwarfing and death of most of the bluestem by 1940. Photo June 23, 1938.

affected by it (Albertson, '38, '39, '41; Albertson and Weaver, '42, '43; Allred, '35, '41; Beath, '35; Bell, '35; Ellison and Woolfolk, '37; Gates, '34; Pechanec *et al.*, '37; Savage, '37; Savage and Jacobson, '35).

Record of Change

The history of the major changes in these prairies is reported briefly and somewhat schematically. Changes in the three prairies may be directly compared by reading each year's story from left to right. The history of an individual prairie may be obtained by reading down the column. The fate of the vanishing dominants is set out in black-faced type, and that of the widely spreading western wheat grass in italics. Hence, either may be followed without reference to the other vegetation. Perennial grasses involved are little bluestem (*Andropogon scoparius*), big bluestem (*A. furcatus*), blue grama (*Bouteloua gracilis*), side-oats grama (*B. curtipendula*), buffalo grass (*Buchloe dactyloides*), western wheat grass (*Agropyron smithii*), and Scribner's panic grass (*Panicum scribnerianum*). In addition are the annual sixweeks fescue (*Festuca octoflora*), downy bromegrass (*Bromus tectorum*), and Japanese bromegrass (*B. japonicus*).

Behavior of Other Species

Indian grass (*Sorghastrum nutans*) completely disappeared at all three stations after the initial years of the drought. Little bluestem entirely disappeared from Clay Center, it was practically exterminated at Montrose, and only poorly represented in the best preserved fragments of predrought prairie at Carleton. June grass (*Koeleria cristata*) never survived under western wheat grass; it was of minor importance elsewhere at Carleton, and rare at the other stations. Tall dropseed (*Sporobolus asper*) was rare at Clay Center but became increasingly common at the other stations. Kentucky bluegrass (*Poa pratensis*), which

CARLETON

Little bluestem furnished 50 to 85% of cover; big bluestem 50% on lowlands but 20% elsewhere. Mixed bluestem type. A few small areas of blue grama and buffalo grass. *Wheat grass was nearly confined to ravines, forming 25–33% of cover locally.* Weeds absent; 35 species of perennial forbs.

Little bluestem suffered 95% loss; big bluestem lost 10 to 15%. Less than 1/4 of prairie was covered with a greatly thinned stand of bluestem; 1/4 was mixed (mostly big) bluestems and wheat grass; *1/2 was dominated by alternes of nearly pure but open sod of wheat grass.* Both short grasses had increased. Sixweeks fescue was abundant in bared places. Large bared areas were occupied by uniform stands of many-flowered aster. Many dead forbs.

Some growth in spring; all grasses dried in July. **Further death of bluestems by drought.** More forbs died. Aster very abundant locally. Ruderals moderately abundant.

Big bluestem dominant only in local but clearly defined patches. *Wheat grass greatly extended its territory (fig. 2).* Side-oats grama increased in abundance. Short grasses extended their local areas and started new ones. Aster greatly decreased. Sixweeks fescue and downy bromegrass were abundant.

Big bluestem remained uninvaded in patches 2 x 3 rods or less in area; one alterne in ravine 5 x 8 rods. It had become less important in the fourth of the prairie where it was intermixed with wheat grass. *Death of relict vegetation resulted in more extensive areas of wheat grass. It had spread over 9/10 of the prairie.* Blue grama increased greatly, patches 1 to 225 sq. yds. in area. Bunches common under wheat grass. Side-oats grama was widely spread in big bluestem areas; it often replaced big bluestem in wheat grass mixture. Buffalo grass increased. *Aster greatly decreased as wheat grass spread.* Pattern of remaining bare soil shown by dense growth of sixweeks fescue, or small alternes of downy bromegrass. Forbs few, dwarfed.

	CLAY CENTER	MONTROSE
1932–33 Moderate Precipitation	**Little bluestem constituted 75 to 95% of cover; big bluestem 50% in ravines but 5–20% elsewhere. Mixed bluestem type.** *A few isolated stalks of wheat grass.* Short grasses were common on dry slopes as alternes or mixtures. 35 species of forbs. No weeds present.	**Little bluestem composed 65 to 80% of cover; big bluestem 98% on lowlands but 5–20% on uplands. Mixed bluestem type.** Side-oats grama often composed 10–15% of cover. *Wheat grass occurred mostly as isolated plants;* occasional clump of short grass. 44 species of forbs. No weeds.
1934, Extreme Drought Examined in 1935, Normal Precipitation	A part of vegetation was buried under 1 to 6 inches of dust; whole prairie dusted. **Little bluestem was all dead. Big bluestem persisted mostly in isolated patches, damage heavy (fig. 3).** Short grasses, where not buried deeply, were thriving. Sixweeks fescue was densely aggregated in patches on drought-bared soil. Aster had increased. *Wheat grass occurred in thin stands on dust-covered soil but as great alternes in driest places; densely aggregated on low ground.* Ruderals abundant almost throughout.	**Little bluestem was reduced to 1%; losses of big bluestem were very severe, only local patches left. In many places 75% of vegetation had died, and even 50% on low ground. Often open stands of big bluestem alone remained. Only 1/3 to 1/5 of basal cover was left.** Short grasses lost least and were spreading rapidly. *Wheat grass stands had appeared, especially in dusted places.* Many dead forbs. Abundant potential weed population.
1936 Moist Spring, Dry Summer	**Continued losses of big bluestem and most grasses.** *Wheat grass grew in nearly pure stands where it invaded earlier, and in widely spread thin ones.* More forbs died. Weeds abundant; dense patches of downy and Japanese bromegrass.	*Fair growth in spring; wheat grass invaded dust-covered areas forming open cover; also patches in ravine.* **All grasses dried in July; big bluestem and others suffered further losses.** Many ruderals.
1937 Moist Spring, Dry Summer	**Big bluestem and most predrought grasses suffered further losses.** *Wheat grass had spread over most of the prairie.* Blue grama bunches occurred widely. Enormous crop of weeds dried in June. Annual bromegrasses dominated much of the lower land.	**Big bluestem and most predrought grasses decreased.** *Wheat grass extended its area.* Short grasses increased. Many weeds. Forbs much reduced in numbers and stature.
1938 Normal Precipitation	*Prairie weedy; wheat grass covered 3/5 of it, more than half being a nearly pure stand, the rest with an understory of bunches of blue grama (fig. 4).* Next largest type was annual weeds on areas repeatedly dusted, last time in 1936. Pure open stands of blue grama were third in area occupied. Very little side-oats grama. **A few small patches of big bluestem remained and widely scattered isolated plants of big bluestem and other grasses were thriving among weeds.** Some nearly pure patches of Pennsylvania sedge. Scribner's panic grass was prominent in pure local stands. Patches of annual bromegrasses suppressed widely scattered perennials. Forbs were much reduced, especially under wheat grass. Aster was the chief weedy forb.	*Prairie a mosaic of types; about 4/10 was pure, flourishing, wheat grass type; 3/10 was covered with wheat grass—side-oats grama mixture,* large distinct bunches of side-oats grama formed half of mixture, but sometimes occurred in pure stands. Remaining 3/10 composed of three types: **(A) side-oats grama and big bluestem, the latter spreading and sharing space of dead little bluestem with side-oats. This type occurred in patches and streaks. (B) Big bluestem which had spread and formed pure stands in relict patches of bluestem prairie;** and (C) blue grama-buffalo grass type well distributed and spreading throughout, also many isolated new stands. Basal cover was still open except under old wheat grass. Sixweeks fescue was abundant. Forbs greatly reduced in species, number, and stature. Annual weeds were scattered sparingly throughout.

CARLETON

Side-oats grama thrived as wheat grass waned; it had invaded or was invading wheat grass nearly over the whole prairie; it was the most important species, wheat grass ranking second. Blue grama and buffalo grass were still increasing. *Pure wheat grass stands were greatly thinned by invasion of side-oats grama and short grasses, or wheat grass was thinly invading short grasses and thus forming mixed prairie (fig. 5).* But pure short-grass stands were common. **Many equal mixtures of big bluestem and side-oats grama.** Also many small pure stands of side-oats grama. **Pure big bluestem had thickened its stand but size of areas had decreased.** Basal cover in general greatly increased, soil mulch reappeared, much less bare ground, weeds few, except bromegrasses in patches. Very little aster. Forbs almost rare.

Much big bluestem had died. Many former mixed patches were now all wheat grass. Largest relict area maintained many prairie species, even little bluestem. All but 1% of side-oats grama had died, forming an open light-colored layer under wheat grass. An exception was 5% left in ravines. Some recovery in fall. *Wheat grass increased greatly; occupied 3/4 of prairie. Stand was thicker, better cover of debris.* Blue grama and buffalo grass increased greatly. Practically no weeds, except large patches of bromegrass. Forbs reduced to 19 species, scarce. *No aster, all of its area was occupied, mostly by wheat grass.* Total yield 0.45 ton per acre.

Big bluestem had decreased. *Periphery of big bluestem alternes invaded 6 to 10 ft. by wheat grass. Wheat grass thickened old stands everywhere, occupied all bare soil, and established thin new growth throughout smaller patches of bromegrass. Also invaded periphery of all larger ones and occurred as small dense patches in them. It had spread into short grasses, especially buffalo grass. This intermingling with and increasing of short grasses had resulted in mixed prairie over 2/5 of entire area.* Side-oats grama was present, mostly sparingly, with a few other very minor grasses. *Overwhelmingly heavy cover of wheat grass with or without short-grass layer.* Total yield 2.43 tons per acre.

CLAY CENTER

1939

DRY EARLY, MOIST IN LATE SPRING, DRY SUMMER

Big bluestem had not increased, injured by drought. Flourishing side-oats was scattered widely but thinly through wheat grass. *Wheat grass was doing poorly, it had increased its areas somewhat but stands were often unconsolidated.* Bunches of blue grama were scattered widely; it controlled about 1/3 of the prairie; often formed an understory to wheat grass (fig. 6). Carex formed two large nearly pure areas. *Some large, half-bare areas were being revegetated by mixed perennial grasses, including wheat grass.* Scribner's panic grass was abundant. Weeds few, dwarfed. Bromegrass was much reduced, permitting fair growth of perennial relicts. Species of grasses and forbs few.

1940

DRY TO MOIST SPRING, DRY SUMMER

Big bluestem greatly weakened or dead. *Wheat grass had invaded the few, small relict patches on all sides, occupied much bare soil in thin stands, and was encroaching on edges of other alternes. Much of wheat grass was of open growth and weed infested.* Considerable open ground in which various relict and invading grasses competed with coarse weeds. Sedge increased. Much side-oats grama had died. Some blue grama died, increased in general, stands open. Bromegrasses thick in their alternes where isolated relict grasses succumbed. A weedy prairie. Forbs reduced to 24 species. Total yield 0.62 ton per acre.

DROUGHT ENDS

1941

WET SPRING, MODERATELY MOIST SUMMER

Drought losses heavy; 95% of remaining big bluestem and nearly all other relict grasses killed. Much side-oats grama, Carex, and even some blue grama died. *Wheat grass was less vigorous but had spread more widely. Except for wheat grass and blue grama, vegetation was composed of annual weeds; 1/3 was weeds or with only a thin growth of wheat grass; no weeds occurred in dense stands of wheat grass.* Bromegrass was dense in its alternes, perennial relicts dead or dormant. *Here wheat grass was slowly invading.* Total yield 2.38 tons per acre. (*In 1942 a good wheat grass—short grass prairie was established.*)

MONTROSE

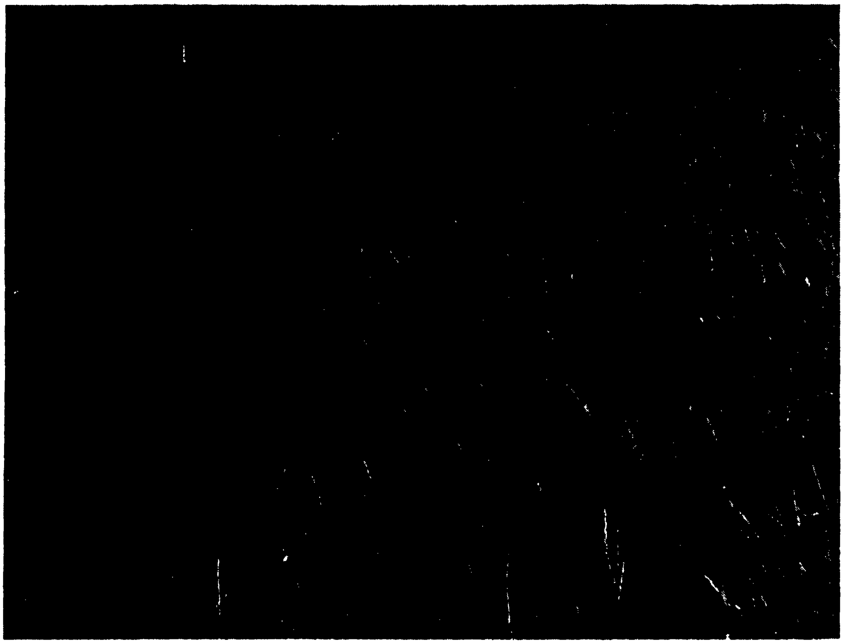
Wheat grass had spread greatly, rhizomes threaded through much big bluestem and side-oats grama territory, thus entering the most mesic sites. Side-oats grama ranked second in importance and was in better condition than wheat grass in this mixture. **Big bluestem was not increasing; it ranked third and was handicapped by drought. Broad alterne on mid-slope reduced to 30 feet in width.** Both short grasses thickened and extended old areas and established many new ones, often under wheat grass. Forbs rare, some dying. Drought severe, half of prairie burned in July.

Big bluestem greatly reduced by drought; relicts small and few; largest alterne had shrunk to 3 to 18 feet in width and a few rods in length. Side-oats grama sparse, not thriving. Short grasses increased greatly with new centers of growth almost throughout; often intermixed with wheat grass. *Wheat grass flourished in spring, thickened old stands, spread everywhere, and replaced nearly all relict big bluestem on north slopes and in ravines. Overwhelmingly wheat grass or wheat grass—short grass prairie.* Other grasses less than 3%. Total yield 0.61 ton per acre. Forbs reduced to 21 species.

Big bluestem nearly gone; largest alterne now fragmented, greatest width 10 feet. *Wheat grass was scattered throughout the largest big bluestem alterne.* Side-oats grama generally decreased, some revived. Short grasses increased rapidly; as in other prairies, blue grama exceeded buffalo grass by 1/2 to 2/3 in amount. *Wheat grass occupied nearly the whole prairie with or without a layer of short grasses.* Debris accumulated. Weeds rare. Total yield 2.78 tons per acre.

occurred sparingly in two prairies and in abundance of 10 to 15 per cent locally at Carleton, was not found at the end of the drought, except very sparingly under the relict big bluestem at Carleton. Sand dropseed (*Sporobolus cryptandrus*) entered the prairies after 1934. It was scattered sparingly, aggregated in a few areas locally, and survived the severest drought. Scribner's panic grass occurred sparingly in relict areas at Carleton, in one ravine only at Montrose, but became an important pioneer in low, dust-deposited soil at Clay Center. There was only a little *Carex pennsylvanica* at Montrose; it exhibited good resistance to drought and increased at Carleton, and developed numerous large dense patches at Clay Center, but declined there near the end of the drought.

Sixweeks fescue was not important at Clay Center, except in 1935; it was scattered lightly in all grass types, but especially in and about short grasses at Montrose. It played its usual important role as an early occupant of bare soil at Carleton. Little barley (*Hordeum pusillum*) was sparse at Montrose, never occurred in quantity at Clay Center, but became abundant in the wheat grass at Carleton. It bulked small, however, compared with its abundance of 1 to 2 tons per acre in the degenerated mixed prairie farther westward (Weaver and Mueller, '42; Albertson and Weaver, '43). Bromegrasses were not common at Montrose but played a prominent part in the subsere at the other stations where dense stands occurred. They utilized large amounts of water, and produced deep shade both when alive and after they had dried and lodged. But they were gradually replaced by western wheat grass and short grasses. Weeds occurred only sparingly in wheat grass, except at Clay Center where they were frequently abundant, especially in 1940. They were, in addition to the weedy grasses, chiefly *Lepidium densiflorum*, *Chenopodium album*, *C. leptophyllum*, and dwarfed *Salsola pestifer*. These



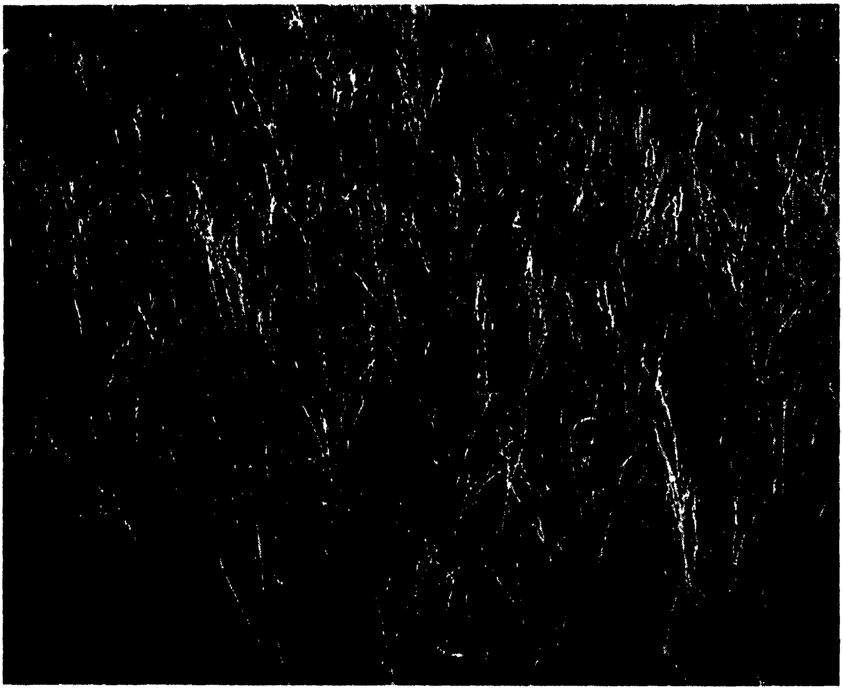


FIG. 4. A pure heavy stand of western wheat grass on low ground on July 15, 1938. The lodged plants form a cover 5 to 8 inches thick. This area at Clay Center was formerly occupied by big bluestem.

FIG. 5. A thin stand of western wheat grass which has recently invaded an area already occupied by buffalo grass and blue grama. Photo of this mixed prairie at Carleton, August 11, 1939.

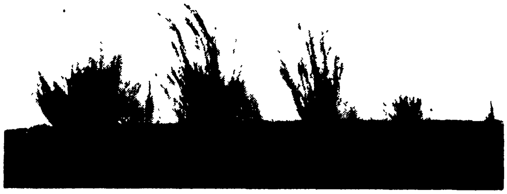


FIG. 6. Various stages in development from seedlings to 3-year-old bunches of blue grama. The 14 plants were obtained in 1939 from a wheat-grass area of four square meters at Clay Center. They represent the early development of the lower layer in mixed prairie.

species also occurred in bared areas especially at Clay Center, but to a less extent at Montrose, being fewest, except bromegrasses, at Carleton. Other important species were *Leptilon canadense*, *Panicum capillare*, *Amaranthus retroflexus*, and *Helianthus annuus*. Weeds were nearly all finally replaced by western wheat grass or short grasses.

Forbs that entirely disappeared included *Meriolix serrulata*, *Psoralea argophylla*, *Salvia pitcheri*, and *Liatris scariosa*. Even plants of *Amorpha canescens*, *Rosa arkansana*, and *Kuhnia glutinosa* died during 1939. *Amorpha canescens* was the only species of perennial forb that persisted well under wheat grass. Two forbs became common at all stations after 1936 and increased year by year until they became very widely distributed and usually extremely abundant. They were *Oxalis violacea* and *Anemone caroliniana*. Both have relatively large organs for food accumulation, bulbs and tuberous rootstocks respectively, and both blossom and produce seed relatively early in the growing season (cf. Resurvey of forbs. Weaver and Albertson, '43).

DISCUSSION

A good development of western wheat grass is dependent upon sufficient available soil moisture in spring and early summer. This grass is of northern extraction and renews activity in this area usually in March. It develops rapidly in April and May, often attaining full vegetative stature and producing flower stalks early in June. Since there was usually little reserve water in the soil during the drought years, growth of wheat grass was nearly always dependent upon spring rainfall (Weaver, '42).

Precipitation from March to May inclusive in 1934, together with water reserves at the beginning of this extremely dry year, seem to have been sufficient to promote a good growth of wheat grass (figure 7). Enough precipitation occurred during this period in 1935, when

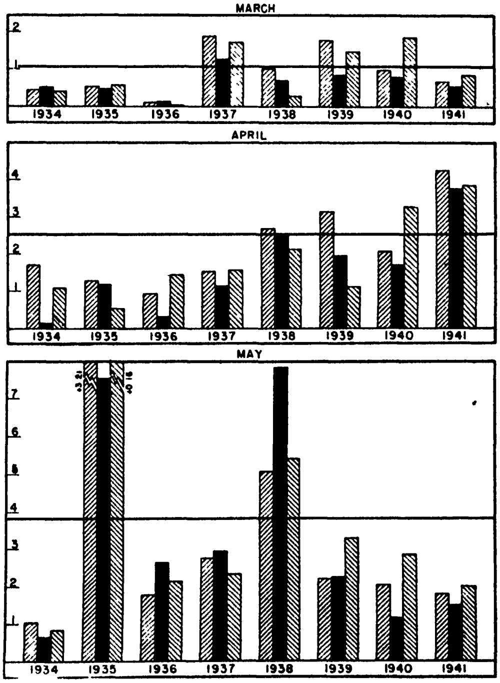


FIG. 7. Precipitation in inches in March, April, and May (1934 to 1941) near the prairies at Clay Center (black), Carleton (diagonal lines at left), and Montrose (diagonal lines at right). Average normal monthly precipitation at the three stations (from which any station varied but little) is indicated by a heavy horizontal line.

competition for water was greatly reduced by death of more mesic grasses, so that the spread of wheat grass was very great. There was a reserve of moisture in the soil following 1935 which coupled with moderate spring rainfall in 1936 promoted its continued spread. Conversely, the low summer rainfall, dry soil, and other conditions of growth were extremely detrimental to later developing grasses. Clay Center, for example, had only 40 per cent of the normal precipitation. A period of drought beginning on June 5 extended for 24 days without rain. A shower of .56 inch then fell but was followed by 37 days with no effective rainfall. Robertson ('39) describes conditions at Carleton as follows: "Four days spent on this prairie in the middle of July, 1936, served to impress one with the severity of physical and biotic factors so extreme that even native vegetation could not endure them uninjured. Daily maximum temperatures ranging from 104° to 111° F. accompanied by relative humidities of 19 to 24 per cent, continuous strong winds, glaring sunlight, and subnormal precipitation combined to make the grasses crackle underfoot like wheat stubble. Only false prairie boneset (*Kuhnia glutinosa*) and blazing star (*Liatris punctata*) appeared unhampered by drought, and they were borne down and partly eaten by hordes of grasshoppers."

In 1937 the moist spring was very favorable to an excellent development of wheat grass. It greatly extended its territory in all of the prairies. Big bluestem, however, already weakened by the previous summer's drought, suffered further losses during the dry summer.

A year of good precipitation, 1938, accelerated the spread of wheat grass. Its dominance was extended even more widely. Side-oats grama which had in-

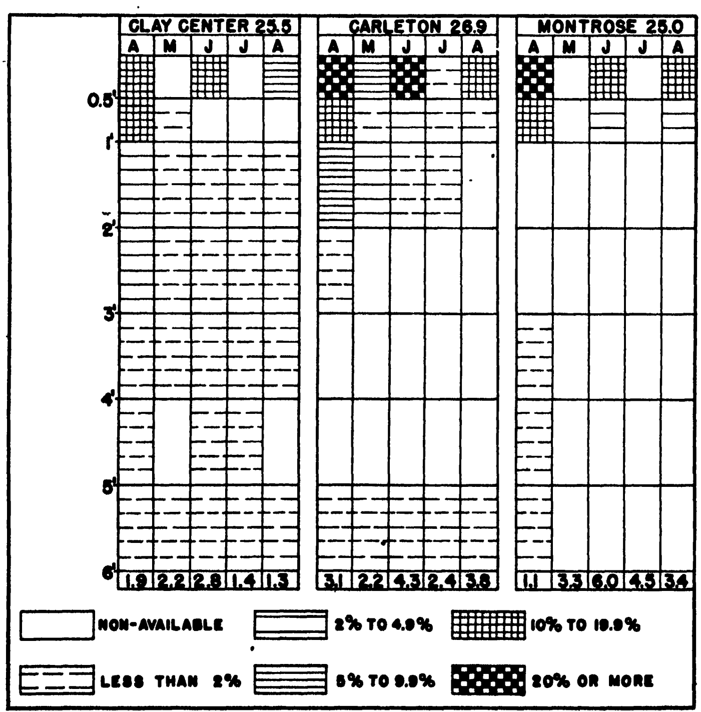


FIG. 8. Available soil moisture to a depth of 6 feet at three wheat-grass stations in 1939. Normal precipitation at each station follows the name, and total current monthly rainfall is given at the foot of each column.

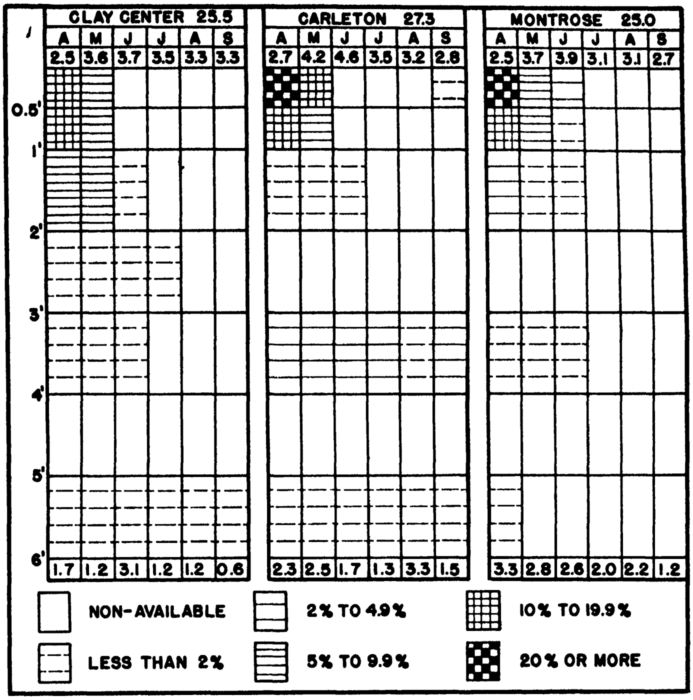


FIG. 9. Available soil moisture to a depth of 6 feet in 1940. Normal annual precipitation at each station follows the name, normal monthly precipitation is below the letter indicating the month, and current monthly rainfall is given at the foot of each column.

creased greatly, distinctly profited also, often by utilizing the space left bare by the death of big bluestem. Vigorous bunches 3 to 6 inches in basal diameter with flower stalks 3.5 feet tall were scattered widely and seed was produced in abundance. There was much bare soil in the aggregate open for colonization. Even big bluestem increased its area locally.

Wheat grass waned in 1939, perhaps in part because of its remarkable growth and seed production the preceding year but partly because of severe competition with an enormous stand of side-oats grama. This occurred following a spring during which the soil was at first dry but later became moist. Summer was dry (figure 8). Although the wheat grass did not produce heads (except where it grew without competition on newly deposited soil) it survived the very dry summer as did the most xeric grasses —blue grama, buffalo grass, and side-oats grama. Finally all of the grasses dried and all green color disappeared from the landscape except that of an occasional deeply rooted forb as *Kuhnia*, *Amorpha*, or *Rosa arkansana*. At Clay Center the vegetation was so dry and drab that it appeared as if it had been frosted.

Wheat grass made good gains in territory during the moderately favorable spring of 1940. Its former competitor, side-oats grama, suffered enormous losses. Disease played an important part (Fowler and Weaver, '40) but death was due also to unfavorable environment (figure 9). Summer was so dry that late in July the remaining big bluestem was mostly dead above ground and reddish brown as is usual in late autumn. Wheat grass was a light tan in color. The vegetation crunched underfoot and would have burned readily. Drought was most extreme at Clay Center where even some blue grama died and where death and deep dormancy delayed recovery in 1941.

The excellent growing season of 1941 (figure 10) permitted wheat grass to complete its dominance in the upper (mid grass) layer. Its heavy foliage and abundant spikes were very impressive. The short grasses had spread slowly to rapidly from year to year almost without interruption and now formed the understory or occurred in the usual small to large patches and alternes characteristic of mixed prairie.

The formation of mixed prairie became clearly apparent in 1938 when an intermixing of wheat grass and short grasses along their numerous ecotones became pronounced. Tufts and small patches of buffalo grass, often on the lower ground, had become common under wheat grass while, usually on the higher land, blue grama was similarly widely scattered in bunches and patches everywhere. Its seedlings survived during periods in the drought years so unfavorable that all others succumbed. Mutual invasion of short grasses and wheat grass progressed in the spring of 1939. It was delayed somewhat at Clay Center by extreme drought in 1940 but became more marked elsewhere. The process was nearly completed over much or most of the prairies at Carleton and Montrose in 1941, but not until 1942 was a good mixed prairie established at Clay Center. In certain other prairies the transition has not yet been completed, patches of true prairie still remaining intact.

The formation of mixed prairie has oc-

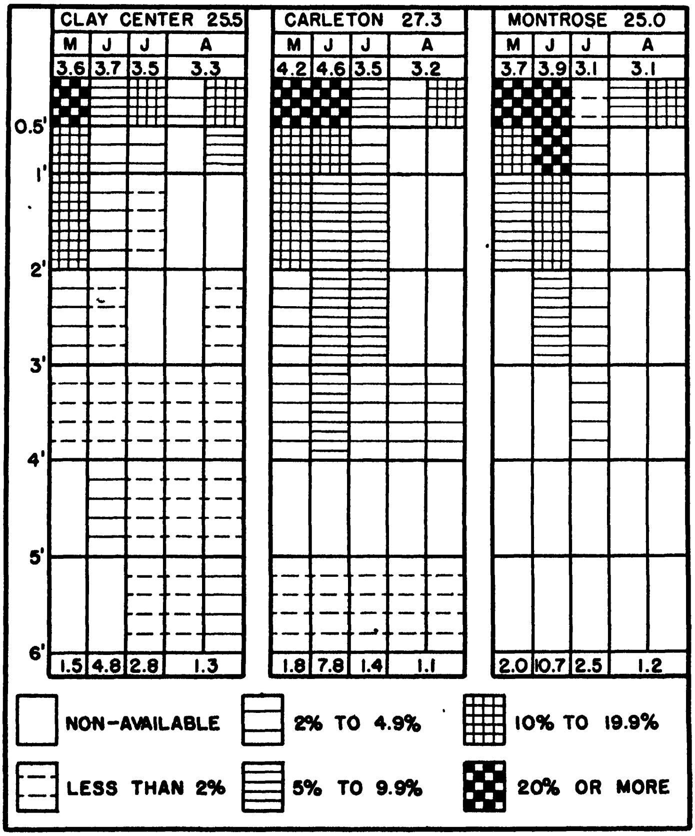


FIG. 10. Normal annual and normal monthly precipitation, current monthly rainfall, and available soil moisture at the Nebraska-Kansas wheat-grass stations in 1941.

curred in the western edge of true prairie throughout a belt 100 to 150 miles in width. Western wheat grass was formerly present in much trampled portions of native pastures and in small amounts along fences. It has swept through pastures as well as prairies with astounding rapidity since 1934. It has often taken nearly complete possession of extensive pastures and ranges (Weaver, '42). This has been accomplished both by wind-blown and rodent-distributed seed and by extensive propagation by long, slender, much branched rhizomes. The rhizomes advanced several feet a year and produced an abundance of new stems, frequently 1000 to 1300 per square meter.

Short grass pastures along the western margin of true prairie have very greatly increased during drought in numbers and in total area. They extend eastward beyond the Big Sioux river in South Dakota and to within 40 miles of the Missouri river in southern Nebraska (Weaver and Hansen, '41). Western wheat grass has become abundant in many of these overgrazed short-grass pastures, especially where stock was excluded for a time. A mixed short grass-wheat grass type has been the result.

SUMMARY

The replacement of true prairie by mixed prairie has occurred as a result of drought in an area 100 to 150 miles in width in central Kansas, eastern Nebraska, and eastern South Dakota. The change of plant populations and structure of vegetation is described in detail as it occurred in three widely separated representative native prairies. Predrought vegetation consisted mostly of little and big bluestem with only small amounts of western wheat grass, side-oats grama, and the short grasses—blue grama and buffalo grass.

The chief dominant, little bluestem, mostly or entirely succumbed to drought in 1934 and 1936. Big bluestem was greatly damaged. It finally nearly disappeared in 1940. Western wheat grass rapidly increased each year. In 1939 it was held in check by an enormous spread and excellent development of side-oats grama. This competitor, however, suffered great losses the following year and wheat grass occupied most of the area. A steady increase and wide distribution of the very xeric blue grama, and, in a smaller degree, buffalo grass occurred synchronously with the rise of wheat grass. By mutual invasions of the mid grass and short grasses, typical mixed prairie became clearly apparent in 1938. By 1941, seven years after the drought began, these grasslands were almost entirely transformed into mixed prairie.

Where native true prairie had been weakened by grazing and trampling, or where it had degenerated to short-grass pasture, wheat grass usually gained even earlier entrance and spread with great rapidity, often resulting in a wheat grass-short grass mixed prairie type.

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POPULATIONS OF THE CHINCH BUG IN THE UPPER MISSISSIPPI VALLEY FROM 1823 TO 1940

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and

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Introduction

Animal population studies on which reports of cycles of abundance have been based in recent years, have lacked many features of detail and accuracy which are desirable. While the studies and reports of chinch bug infestations partake of these imperfections, the writers believe that they possess considerable advantage and better accuracy than many similar population histories. This because it is possible to take into account the total area in which the populations were large, small, or below the crop damaging level. Hitherto only variations in different localities have usually been noted (Chitty and Chitty, '42). Furthermore, the influence of weather conditions on the chinch bug has long been known, frequently verified by field observations and checked in laboratory studies, which is of great assistance in interpreting the cyclic phenomena involved.

The chinch bug, ***Blissus leucopterus*** (Say), is a small dark-colored, white-winged heteropteron insect about three mm. in length, which occurs in two forms —short winged and long winged. The insect is well known by name and reputation throughout the United States and Canada because of its destruction of cereal crops. The first known outbreak of the short-winged form was in North Carolina. There have been repeated outbreaks of the long winged form in the upper Mississippi basin since agriculture began there about 1820. This paper deals with the long winged form in the upper Mississippi basin.

It is believed to have been originally distributed over the United States from eastern Colorado to the Atlantic and from the extreme southern edge of adjacent Canada south to the Gulf of Mexico and into Mexico along the Gulf coast for 300 miles. There are also scattered records for the west coast of the United States, from the savanna and cultivated country of Central America and the West Indies. Its autumnal flight and its occurrence in grass patches often near woodlands gives it a wide territory containing suitable places to live.

The range of large populations of long winged chinch bugs includes our mapped area and extends into southeastern Minnesota, covers most of Iowa, all but the southern part of Missouri, the southeastern part of Nebraska, the eastern part of Kansas, and a strip southward part way across the center of Oklahoma. It thus partly surrounds the Ozark uplift with a semi-circular front facing southeast. The area probably coincides with the original distribution of large chinch bug populations. The range is similar to that of the prairie deer mouse (*Peromyscus maniculatus beardii* (H. and K.)) which lives in similar places.

The original vegetation of the region was tall grasses such as *Andropogon scoparius* (Michx.), *Andropogon furcatus* Muhl., *Koeleria cristata* L., *Sporobolus asper* (Michx.), *Stipa spartea* Trin., etc. To the westward there were large tracts of grassland. Near the center of the area the grassland was interspersed with

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* Dr. W. P. Flint died during June 1943. (Editor)

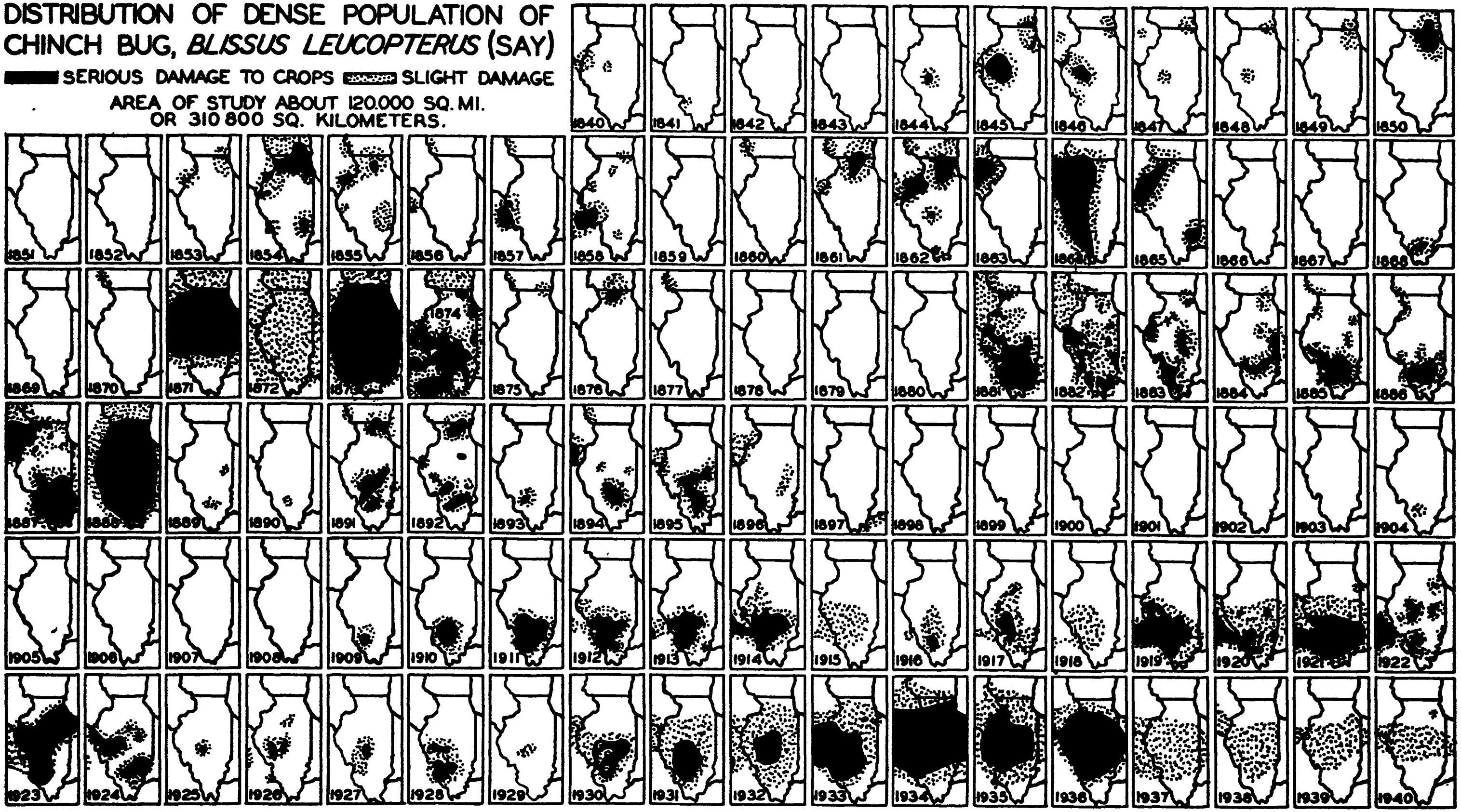

FIG. 1. Showing the distribution of damaging populations of chinch bugs on 120,000 square miles (310,000 km.²) area for 101 years, 1840 to 1940 inclusive. For a discussion of the number of individuals corresponding to severe and slight damage see text, page 437.

forests, chiefly of oaks, along nearly all streams, and dotted with groves of forest. In the eastern end of the prairie peninsula, forests predominated and grassland occurred in islands. The clearing of the land and planting of grains and corn has doubtless led to a great extension of chinch bug range east of our area of study.

AREA OF CHINCH BUG POPULATION STUDY

The Illinois State Entomologist's Office, and its successor, the State Natural History Survey Division, has kept records of the location, area, and degree of chinch bug damage since 1882. Within the State of Illinois, which is the center of the frequently damaged area, the studies and mapping of abundance were carried on for more than 32 years under the close supervision of the late Dr. S. A. Forbes. In 1889 he prepared a summary of the outbreaks in Illinois and surrounding areas, known to agriculturists to that date. The mapping since 1914 has been in the hands of the junior author of this paper. The office has for many years kept maps showing the location of heavy populations and the amount of damage.

While the states adjacent to Illinois usually have not kept as complete records there have been less frequent but extensive outbreaks in the surrounding states of Wisconsin, Iowa, Missouri, Kentucky, and Indiana. The more important of these outbreaks are described in published accounts in terms of crops damaged. In addition we have had the cooperation of the entomologists of adjacent states in the chinch bug population evaluations, especially in those outbreaks of recent years. Their contributions are acknowledged in connection with the maps and elsewhere (fig. 1).

Since south central Illinois is probably the most frequently infested of all the localities in the range of chinch bug damage, with frequency of large populations greater toward the west than toward the east, we have selected an area 270 miles (430 km.) wide from east to west and approximately 450 miles (730 km.) long from north to south. Its center lies about 75 miles (120 km.) northeast of St. Louis, Mo.

The area of 121,500 square miles (315,000 km.^{2}) includes a portion of Lake Michigan and other areas which are not compatible with the life of this insect. Accordingly, 1500 square miles were deducted from the total, for the water, etc. Thus the territory of study includes about 120,000 square miles (312,000 km.^{2}) which may be infested with this insect. To bring out the area relations which the chinch bug population illustrates, a series of maps indicating the location of infested areas from 1840 to 1940 inclusive has been prepared (fig. 1).

The amount of crop damage was recorded by counties in Illinois and the adjacent states. Counties average approximately 670 square miles (1,742 km.^{2}) in area. The area of most general presence of large populations of chinch bugs has its center about 10 miles (16 km.) east of the junction of the Missouri and Mississippi Rivers, 90° 10″ W. Long., 39° N. Lat., that is, 25 miles (40.2 km.) north of the center of St. Louis, Missouri (fig. 2). (See also fig. 7.) It extends about 120 miles (192 km.) in all directions from this point. Crop damage has been reported in the 120,000 square mile area in 88 of the 118 years since the first record in 1823. Only 12 small areas of damage have been recorded wholly outside this radius in 8 years when there was none inside the 120 mile radius. In other words, damage is recorded within this area in 80 of the 88 years of crop damage. In 53 years, the damage was wholly or chiefly within this area, being confined to it in 16 years. Damage occurred within the 120 mile radius in 15 years in which only the smaller part was limited to it. These years include nine in which the damage was widespread.

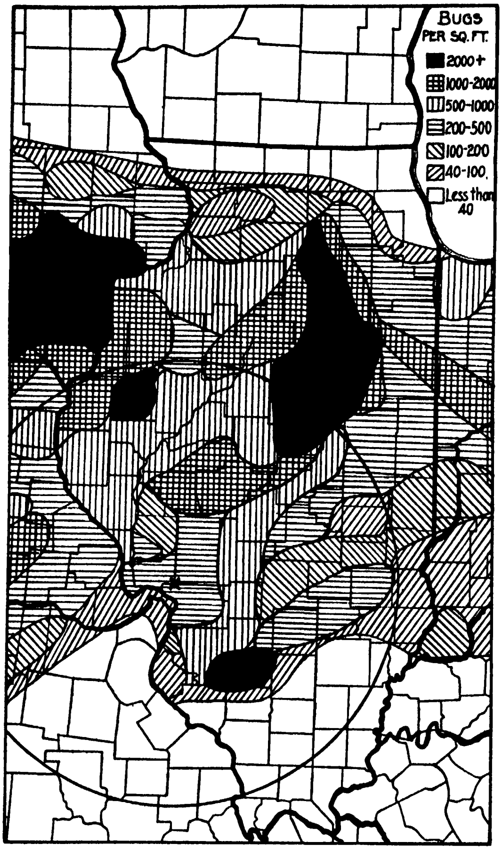

FIG. 2. Showing the numbers of bugs in hibernation in the winter of 1939–40 in Illinois and surrounding areas, by counties. There were usually about five observations per county. Each observation consisted of two samples of one-fifth square foot, chiefly in bunch grasses belonging to the genus Andropogon. The circle encloses the area most frequently suffering crop damage. The radius is 120 miles around the point marked "X."

FOOD PLANTS AND ESTIMATION OF POPULATIONS

Herbs of the grass family (Gramineae) are the only plants of any importance as food of the chinch bug. Wild annuals, especially selected as favorites, are fox tail (*Alopecurus carolinus* Walt.) and crab grass (*Syntherisma ischaemum* (Schreb.) Nash.), both common in waste places under agricultural conditions and on flood plain deposits and eroding bluff under natural conditions. Blue grass is not favored by the bugs but is used to some extent. For winter shelter, wild grasses of the genera *Andropogon* and *Sporobolus* are important.

Damage to crops falls on three types, namely small grains, Indian corn, and cultivated grasses. Small grains are damaged in the spring and early summer. Of cultivated plants, oats are least attractive to the bugs (Benton '38). Forbes ('89) published a complete survey of the 102 counties of the State of Illinois for the year 1887, by townships, with categories ranging from no damage to complete destruction. The report was divided into damage to small grains, Indian corn, and grasses, a total of 2640 items (townships usually 36 miles square, 93 km.^{2}). This is an average of 26 reports per county. The total possible number was probably 50 to 60. This paper emphasizes the food plant preferences although he classed rye, wheat, and barley together. Moreover, Benton points out that the condition of plants such as the stage of development, lushness, etc., is important. Maize or Indian corn is a favorite mid and late summer food. In late summer and autumn, annual grasses and Kaffir corn are used.

In cultivated areas the adult insects hibernate in the bunch grasses on the south-facing slopes of road cuts and in the edges of woodlands under debris and in smaller concentrations in all sorts of places near the surface of the soil where they aggregate as a result of a general dispersal flight to winter shelter which takes place on the closing hot days of autumn. During April and May they leave the hibernating quarters and migrate on to winter wheat or other small grains, where they produce the eggs and nymphs. The early nymphal stages are bright red. As the animals approach maturity, the body color shifts to maroon, to dark brown, and terminates in black in the last nymphal and in the adult stages. The adult body is partially covered by the translucent nearly white wings. As the wheat or other small grain begins to ripen and become dry, the nymphal stages leave the wheat fields and migrate into Indian corn fields where the second generation of nymphs commonly appears. In this migration the nymphs may travel 0.25 of a mile (.42 km.) or more. In this process of migration they often literally darken the soil and can be gathered by the bushel in vertical cylindrical holes 6 inches (15 cm.) in diameter such as are made for setting posts. All sorts of mechanical methods, usually consisting of a system of trenches and the use of chemicals, have been devised for stopping this migration. After leaving wheat the insects feed on the Indian corn until it becomes somewhat dry as a result of maturity, when, in the southwestern part of their range, they often move to Kaffir corn or annual grasses, where in favorable years there may be a third generation.

The populations counted or estimated represent what Elton ('32) has called economic densities or densities in that portion of the area in which the animal can live. In general, areas of water, forest, and areas occupied by roads, buildings, etc., are not inhabited by chinch bugs except incidentally. Accordingly, estimated populations do not cover these areas. Within the areas inhabited by the bugs, many population estimates have been made both in hibernation areas and on field crops.

Numbers on Small Grains.—In the last serious outbreak (1934–1937), Benton ('38) made counts reported as the number of bugs per linear foot of grains in drill rows four inches (10 cm.) apart. There are 16.4 feet of linear row in a square meter (10.76 square feet).

According to Benton's work more than 400 bugs per square meter (37 per square foot) may be counted on to do severe damage to grain.

This general conclusion is supported by the records of J. H. Bigger of the Illinois State Natural History Survey Division. About May 18, 1933, he found wheat with 605 and with 408 bugs per m.^{2}, very thin. In June, 1935, he found wheat in poor condition with 432 bugs; excellent with no bugs, and fair with 147 and 112. In general, wheat with no bugs was noted as very good or excellent. Since the bugs move to the best nearby food, there was one record of wheat in poor condition with a note, "adjacent volunteer wheat heavily loaded with bugs," suggesting that migration had taken place. In considering damage it is finally expressed in terms of the effect on all crops during the season. With the enormous reproductive and survival capacity in favorable years, the numbers of bugs reach 40 or more times the number of breeders occurring in May and early June, with a corresponding possibility for causing damage.

Numbers on Corn.—Thomas ('79) calculated numbers in corn fields based on counts, estimates, etc., of the number of bugs on two and one-half acres (1 hectare). Corn is ordinarily planted in groups of three seeds, 40 to 42 inches apart. This places one group of two or three plants approximately in the center of each square meter (39.4 inches on the sides). Thomas estimated a maximum of 17,000 individuals to a hill of corn (per m.^{2}). The migration from wheat to corn may cover one-fourth mile (402 meters), and the ground between the two fields

TABLE I. *Chinch bug census*

Locality	Date	Per square foot	Per m.^{2}	Rating
Aurora, Illinois	May 11–26, 1934	74	792	Severe
Sterling, Illinois	May 15–25, 1936	1	10	Slight
Sterling, Illinois	May 31–June 12, 1935	36	390	Slight–Moderate
Taylorville, Illinois	May 15–June 4, 1937	6	64	Slight

is densely covered with moving bugs. He computed the population in corn as 175,000,000 bugs per hectare, or 70,000,000 per acre. This density of population is a number sufficient to cover the surface of a strip 40 rods (200 meters) long and one rod (5 meters) wide with the heavy density often observed during migration. This number would be reached on 2.5 acres or one hectare (50 × 200 meters), for each section of the migrating population covering the area between two fields, but Thomas failed to state how many sections pass over the area or in other words the duration of the migration.

Thomas' statement appears to be hypothetical as regards the number of bugs (17,000) per hill of corn or 5700 per plant. The space available for bugs on a corn plant must be considered. Montgomery ('16) states that the *leaf* surface of a corn plant is 1152 square inches (eight square feet) or 7432 cm.^{2}, to which should be added 968 cm.^{2} (150 square inches) for the stalk and 380 cm.^{2} (59 square inches) for the leaf sheaths, making 8780 cm.^{2}. Four adult bugs can rest on a square centimeter (25 per square inch) without touching each other, thus making space for 35,120 per plant, and with three plants to the hill the total space would accommodate 105,360 bugs per hill which is six times the number estimated by Thomas. This is conservative as Luginbill has found an average of 285 fourth and fifth instars per square inch (official communication). A plant with 8780 square centimeters would probably be larger than those to which the chinch bugs would migrate when they leave the wheat, and also many of the bugs would be smaller than adults. Five thousand seven hundred bugs per plant are probably enough to destroy the plant, but would cover only about one seventh of its surface, chiefly its lower portion and the leaf sheath and base. Philip Luginbill stated in an official communication, on the basis of counts he has made, that Thomas' figures are entirely reasonable. Temperature and rainfall not only influence the insects but also influence the number of individuals a plant can support without wilting and losing vitality beyond recovery.

Number in Hibernation.—For many years censusing of hibernating bugs has been the general practice of the Illinois State Entomologist's Office and its successor, the State Natural History Survey Division. In times of threatening outbreak other states and the United States Bureau of Entomology and Plant Quarantine followed a similar practice. A general survey was made in the autumn of 1939, the states and federal authorities cooperating. At this time the bugs are concentrated in litter of fence rows, the edges of woodlands in the dry bunch grasses, especially Andropogon and Sporobolis. A sample of grass 0.25 square feet in area (0.024 m.^{2}) is taken with a metal frame as a guide, and examined in the laboratory. In some states a 0.2 square foot sample (0.0198 m.^{2}) is taken.

Figure 2 shows the results in the form of a map. Experience has shown that if weather is favorable in the spring, and there are more than 200 bugs per square foot (2000 per m.^{2}) in hibernation, there is danger of severe damage to crops the following year, especially within the 120 mile radius from near the junction of the Missouri and the Mississippi Rivers.

Information on hibernation is important in predicting the possible damage the following year. In many cases, however, the insects are very abundant in hibernation, but little or no damage occurs the following summer due to unfavorable weather in the spring.

Limits of Population Fluctuation.—The fluctuation of numbers between minimum and peak populations differs in different localities, because bugs may almost entirely disappear on the outskirts of the areas of average heavy populations. In the area of 120 miles (192 km.) radius noted above, populations may vary from 4 to 17,500 per m.^{2} (10.7 square feet) (40,000 to 175,000,000 per hectare, or 16,000 to 70,000,000 per acre). The gross estimation for purpose of mapping (fig. 1) has been based on crop damage.

TABLE II. *Criteria of abundance used in this paper. Figures are numberes per M^2.*

Slight (in mapping)		Severe (in mapping)	
		Moderate	Severe
On small grain	10–399	400–600	600+
On corn	400–2000	2000–4000	4000–6000+
In hibernation	10–60	60–400	400–6000+

Within the area inside the 120 mile radius, Fig. 2 and Fig. 7, pages 438 and 447, the standards of damage are lower than elsewhere. Thus, severe damage outside this area was considered as equivalent to moderate within it. However, for convenience in mapping, all moderate and severe damage was classed as severe.

RELATION OF POPULATION AND DAMAGE TO WEATHER

The annual rainfall of the 120,000 square mile area (fig. 2) varies from 25 to 40 inches (65–100 cm.). The April to September (inclusive) rainfall varies from 21 to 25 inches (52–62 cm.) but is quite similar in Illinois and central Oklahoma.

The normal spring rainfall in this area of most frequent damage is a little more than four inches (10 cm.) for both May and June. The area east, north and southeast of the 120 mile radius is outside the prairie peninsula and in the deciduous forest. Here June rainfall is higher than May rainfall and in some Wisconsin and Indiana areas it reaches an average of five inches (12.5 cm.), while that for May is considerably less than four inches (10 cm.). The same is true of points in northeastern Kansas and eastern Nebraska. In the eastern two-thirds of Oklahoma and Kansas the May rainfall is higher than that for June.

General Relations to Weather.—During the past 75 years, the importance of weather to the chinch bug has been so often observed and published that only the exceptions, real or apparent, need to be considered. The field observation has been confirmed for hundreds of localities. The fact that heavy May or June rains nearly always bring an end to the offspring of a large over-wintering population has especially impressed agriculturists because the crop damage is usually completely or largely eliminated at a time when it is expected. The apparent exceptions might be found to be in accord with the known facts if all information were available. In fact, an "early" spring and very favorable dry April may, in southern localities, take the place of a dry May. Again in a "late" season, late June rains destroy the young bugs. Other combinations of spring weather may be either beneficial or detrimental to these insects. Certain types of autumn weather appear to be favorable to bugs, while others are not. Low winter temperatures appear to have little effect on the populations under Illinois conditions, but are credited with considerable effect in Iowa and Kansas.

The difficulty with attempts to correlate biological phenomena and weather are threefold:

First: Weather stations are much too far apart and, as a result, fail to show what happens in the large areas between them.
Second: The summaries are based on calendar months, which are periods at least twice as long as they should be.
Third: A lack of knowledge of the life history of the animals concerned is usually evident.

The application of these difficulties to the chinch bug problem falls under the following headings:

(*a*) The character of the rainfall is spotty.
(*b*) The monthly summaries cover more than twice the length of the first two and more sensitive instars.

(*c*) The spread of the egg-laying period in any population varies and is not known.

To take up these three difficulties, we may well begin with the most serious one, namely the spotty character of rainfall. This is well illustrated by the study made by the Soil Conservation Service under the direction of C. W. Thornthwaite ('37).

Local Character of Rainfall.—The local character of rainfall is brought out by the records from the scattered stations operated by the U. S. Weather Bureau and illustrated in figure 3. There is occasional evidence of a much smaller scale spottiness in the records of closely placed stations of the Weather Bureau. For example, in the critical chinch bug months preceding and following the winter of 1888–89, there was from 0.6 to 2.04 inches difference between monthly accumulations at the Chicago and at the Evanston, Illinois, stations. They were 11 miles apart, Evanston being due north of Chicago. Recent studies of Thornthwaite ('37) bring out the irregular distribution of rainfall when stations are about three miles apart. The results as regards distribution are shown in figure 3. The study was made in Blaine, Kingfisher, and Logan counties, Oklahoma. The accumulated rainfall of April 26th is shown for the west half of the row of counties while that of the 27th is shown for the east half. The maximum rainfall for Blaine County was 2.00 to 2.50 inches, located in the center of an area of 20 square miles with a rainfall of 1.50 to 2.00 inches. The maximum was at a point seven miles northwest from the station at Watonga, while the station recorded a total of only 0.32 inch. In Kingfisher County the maximum rainfall was 0.10 to 0.25 inch in an area of 12 square miles, while the Kingfisher station showed only 0.06 inch. The rainfall at the Guthrie station was 1.17 inches up to 7:00 A.M. on the 27th, the rainfall for ten miles to the northeast was 1.50 to 2.00 inches or more, and over an area about two miles square 12 miles northeast, 2.5 inches. A large area beginning 15 miles to the southwest had about 0.1 inch of rainfall up to 7:00 P.M. on the 27th. The essential features of the storm of April 26th and 27th are brought out by the maps (fig. 3). Other maps presented by Thornthwaite show a similar spottiness in a storm on May 1st. when Kingfisher County received most of the rain and Logan County (see fig. 3a, 3b) had a second wetting. The wind velocity at the time of the heaviest rainfall near Kingfisher reached more than 30 miles per hour. Heavy rainfall at other points was accompanied by much lower velocities. The high wind velocities tend to kill more young bugs than the low

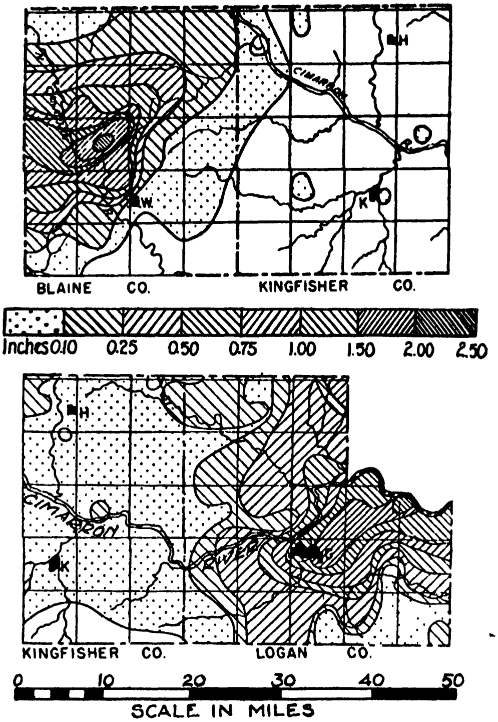

FIG. 3. Showing the distribution of rainfall in three Oklahoma counties during the storm of April 26th, upper figure, and April 27th, lower figure, in 1936. W, K, and G mark the location of three regular weather stations. Kingfisher (K) received less than 0.1 inch while seven miles northwest 2.5 inches of rain fell. (After Thornthwaite, '37. For explanation see text.)

velocities. This introduces another factor likely to lead to local differences in population.

Rainfall Summaries and the Length of the Egg-laying Period.—The two remaining difficulties noted above are the spread of egg-laying within the population and the two great lengths of time covered by weather summaries.

The length of the egg-laying period in a given population of spring breeders is not known but experience shows that it probably varies from 14 to 21 days for the vast majority of bugs.

The earliest date on which the State Natural History Survey and its predecessor have found eggs in any year is April 24th, in 1913. The latest date in any year was October 2nd, in 1918. It appears safe to state that in the average year eggs can be found from the 1st of May to the 20th of September. In some years they may be found in October. The same will hold for nymphs, that is, the earliest date on which we have ever found first instar nymphs was May 17th, in 1896, and the latest date, October 23rd, in 1934. These dates suggest an overlapping of the egg-laying of different generations.

Attenuated egg-laying and overlapping generations can come about through the slowness with which those insects which happen to hibernate in cool, protected spots in woodlands leave for the small grain fields. Thirty days may readily elapse between the movement of the bugs from bunch grasses on south-facing slopes and of those located in woodlands. Extension of the period of departure from hibernation quarters may be brought about by alternation of warm and cold periods which accelerates the advantage of more favorable location. The effect is similar on egg-laying and the emergence of sensitive nymphs. Females emerging from favorable hibernation locations may become mature and deposit eggs. A period of cold weather will hold other females in hibernation while the eggs of the first are developing slowly.

Temperature influences the rate of development, low temperatures very markedly, and may double the rate with a change of 3 to 6 degrees as indicated by the rate chart of eggs and first stage nymphs of Shelford ('32, pp. 507 and 508). For chinch bug work, weather summaries should be made weekly or, at longest, fortnightly. The necessary data are available in recent weather reports, but to compute it in the form of weekly accumulated rainfall is a forbidding and hopeless task except where the state of the bug population is ascertainable. Also, to evaluate the effects of the storms of short duration it is necessary to know at what time within the sensitive period the heavy rainfall came.

Relations to Annual Rainfall and Temperature.—Turning to these relations, Thomas ('80) pointed out that the great outbreaks occurred when low annual rainfall was accompanied by high mean annual temperatures. Checking Thomas' graph (fig. 4) of rainfall against figure 1 shows that the favorable combination occurred in 1840, 1854, 1860, 1871, 1874. By using rainfall and temperature data for the entire State of Illinois, from the U. S. Weather Bureau published data 1878 to 1940 inclusive, to give the same basis as that given by Thomas, figure 4 was constructed. Thomas' figure is repeated at the top section covering 38 years. The bottom section covers 25 years. The drawing follows the plan started by Thomas, who used the data for "Illinois and immediately adjoining portions of Iowa and Missouri" because both the history of the pest, and the weather data were better known in this area than for other portions of the chinch bug area of damage. The area considered is essentially the same as his. The number of stations was limited, and Thomas does not enumerate the area other than in the southern portion. He states that his averages for 1873 to 1877 are from Chicago, Dubuque, Davenport, and St. Louis. Thomas used 50.80° F. or the mean for the stations which he

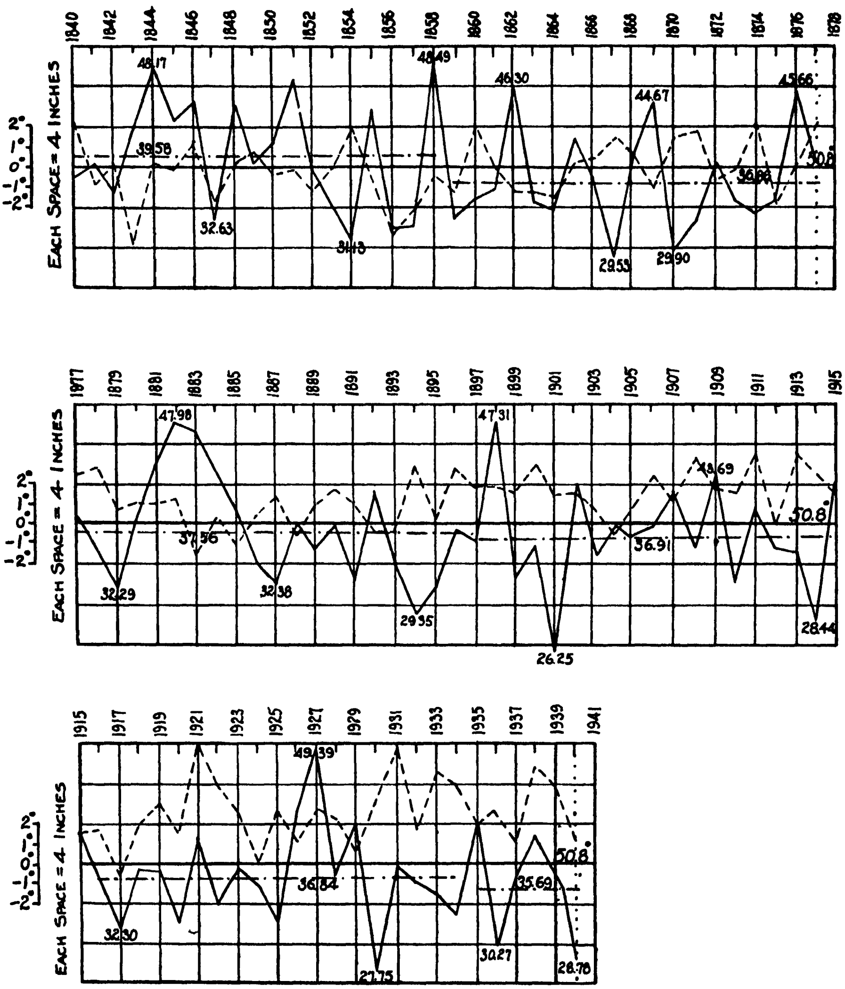

FIG. 4. Diagram showing weather conditions important to the chinch bug for 102 years, 1840 to 1941. Thomas' 1880 weather diagram extended to 1940 using average rainfall and temperature for all of Illinois after 1878. The annual rainfall of the 19 year periods declined from 39.58 inches (100.05 cm.) to 36.84 inches (93.58 cm.) during 95 years.

averaged. Mosier ('03) computes the average for the state to be 52.3° F. Both used stations just outside Illinois. The Weather Bureau summary (Climatological Data) for 1938 gives 52.7°. These are 1.5°–1.9° higher than the means used by Thomas. That is probably due to the preponderence of northern records in his data.

An examination of the century long curve (fig. 4) shows that Thomas' contention of a declining rainfall is borne out. Furthermore, his contention that outbreaks follow years with temperature above normal and rainfall below normal is confirmed. However, it may require several years with this favorable type of weather for the chinch bug population to build up. The year 1930 was one of high temperature and low rainfall, but was not followed by a year of chinch bug damage. However, the chinch bug population started to build up in that year and reached a point in 1934 which caused some of the most serious damage on record. Thomas stated that two dry years were necessary, which is generally true though three are evident in some cases.

Autumn Temperature and Rainfall.—The discussion to this point has covered the effects of annual rainfall. Suggested effects of late summer and autumn conditions and May and June rainfall remains for further analysis. For example, in the late summer and autumn of 1938 conditions were favorable for the development of a large population of bugs. Figure 5 shows the distribution of bugs in hibernation in the winter of 1938–39 which resulted from the unusually suitable conditions.

The temperature and precipitation of the stations within the area where more than 1000 bugs per square foot (10,764 per m.^{2}) occurred were analyzed. The rainfall was 0.75 inch above the normal for central Illinois in July, 1938, but approximately one inch below in August, September, and October of this year. Temperatures were above the normal as follows:

July	3.1°
August	5.6°
September	3.1°
October	8.2°

Figure 6A is a climograph of the chinch bug year in which this late summer increase in population occurred only to be wiped out the following spring. The heavy rainfall in the form of almost daily precipitation between the 20th of May and the 15th of June reduced the bugs to a point where damage to crops was slight.

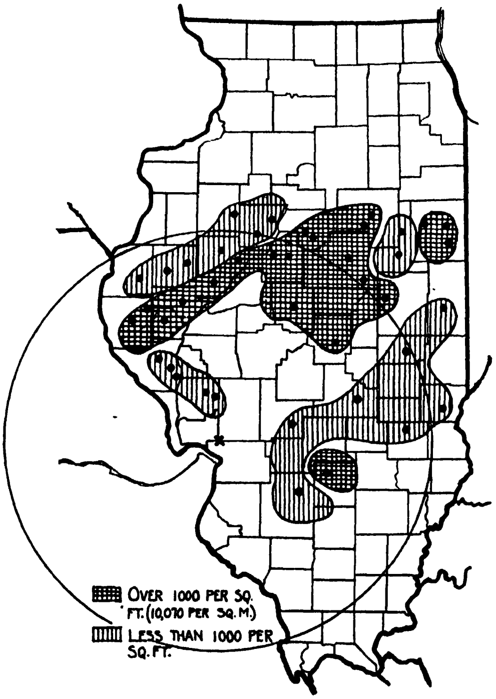
▦ OVER 1000 PER SQ. FT. (10,070 PER SQ. M.)
▥ LESS THAN 1000 PER SQ. FT.

FIG. 5. Showing the points of observation of the distribution of bugs in hibernation in the autumn of 1938 when favorable late summer and autumn resulted in a very large overwintering population. Weather stations in the area with more than 1000 bugs per square foot (10,070 per m.^{2}) were used as a basis for the diagram shown in Fig. 6A.

Examples in other years are analyzed in a series of figures, beginning with 6B showing the conditions in 1913–14 near St. Louis, Mo. (Mascoutah, Illinois). Both late summer and spring conditions were favorable to chinch bugs and the damage was very severe. Figure 6C shows a similar condition.

Winter Conditions.—Alternate mild and severe cold weather during the winter months has been believed to be detrimental. Webster reports published instances of bugs, submerged for a week in water frozen over at the surface or thawed from ice crystal, that became active in a warm atmosphere. He also quotes work done at the Maine Agricultural Experiment Station in which repeated freezing and thawing lessened the cold resistance. He concludes from all the known records that freezing in a moist atmosphere is not fatal but freezing in water or in a dry atmosphere is fatal to bugs. In general a late first autumn frost is beneficial as it keeps food plants in good condition.

Autumn and Spring Temperature and Rainfall in Favorable Combination.—The crop damage by bugs in 1922 in relation to the bug population (crop damage) in

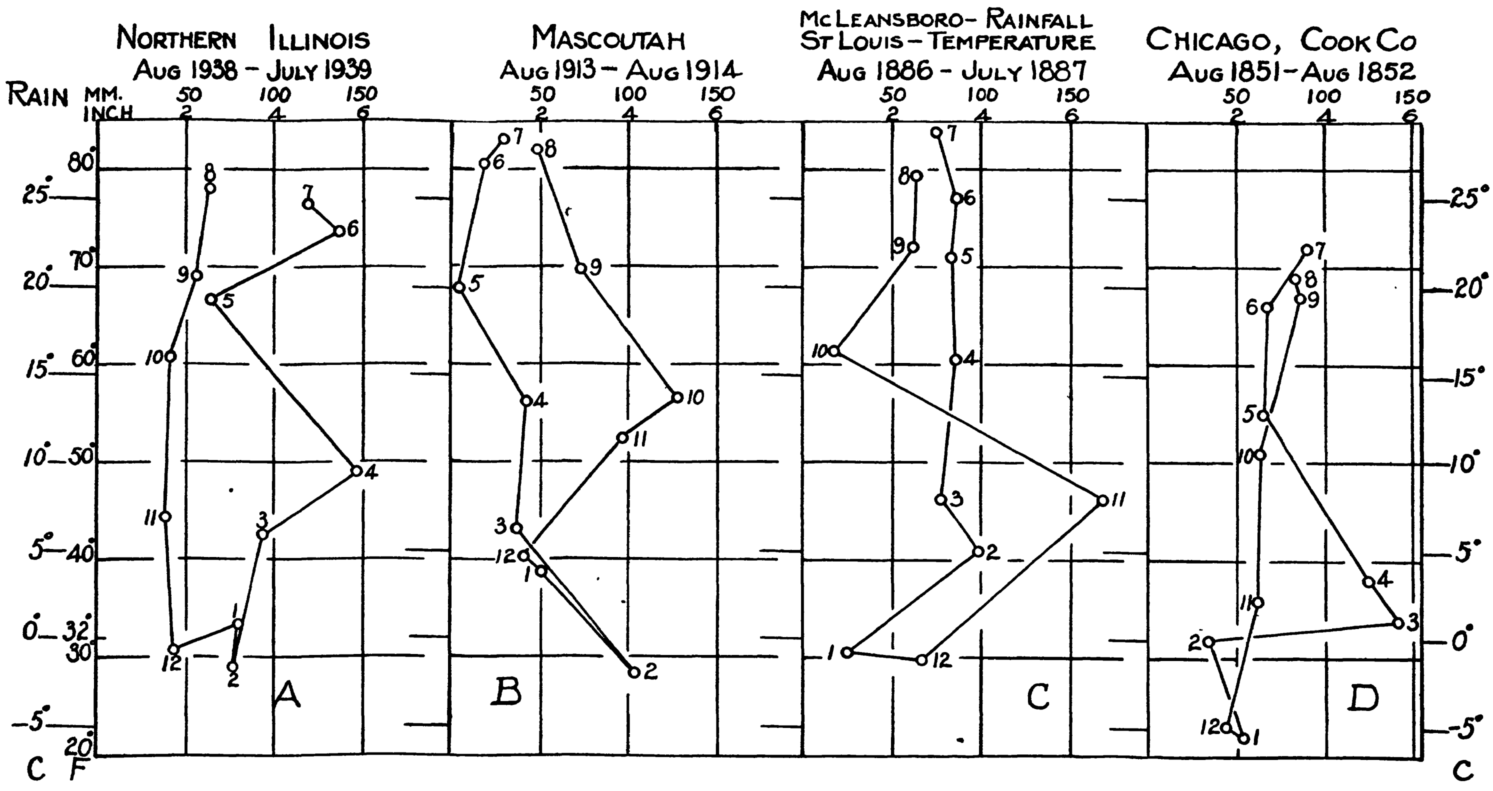

FIG. 6. Climographs of annual weather. A. Showing the weather conditions during and following the favorable autumn of 1938. Populations reached unusual density in autumn but the bugs were killed off by May rainfall. B. Weather at Mascoutah, St. Clair County, Illinois, where a large population of bugs occurred in 1913. A favorable late summer and a very favorable spring gave a large population which resulted in severe crop damage. C. Favorable year at McLeansboro, Illinois, 1886–87. Severe damage occurred in 1887. D. Cook County, Illinois, Chicago. No bugs, favorable autumn and favorable spring resulted in no damage.

1921 and the rainfall in critical intervening months is shown in figure 7A, B, C, and D, and will be discussed with reference to the three clear white circles which will be located in the area of infestation of 1921. Most of the apparent discrepancies are explicable on the basis of the May and September rainfall which is noted in the text. The explanations are based on the fact that heavy rains are detrimental to the insect concerned.

The low June rainfall permitted the survival of bugs over much of the area mapped. (Compare C and D of fig. 7.) Survival through August rainfall (fig. 7D)

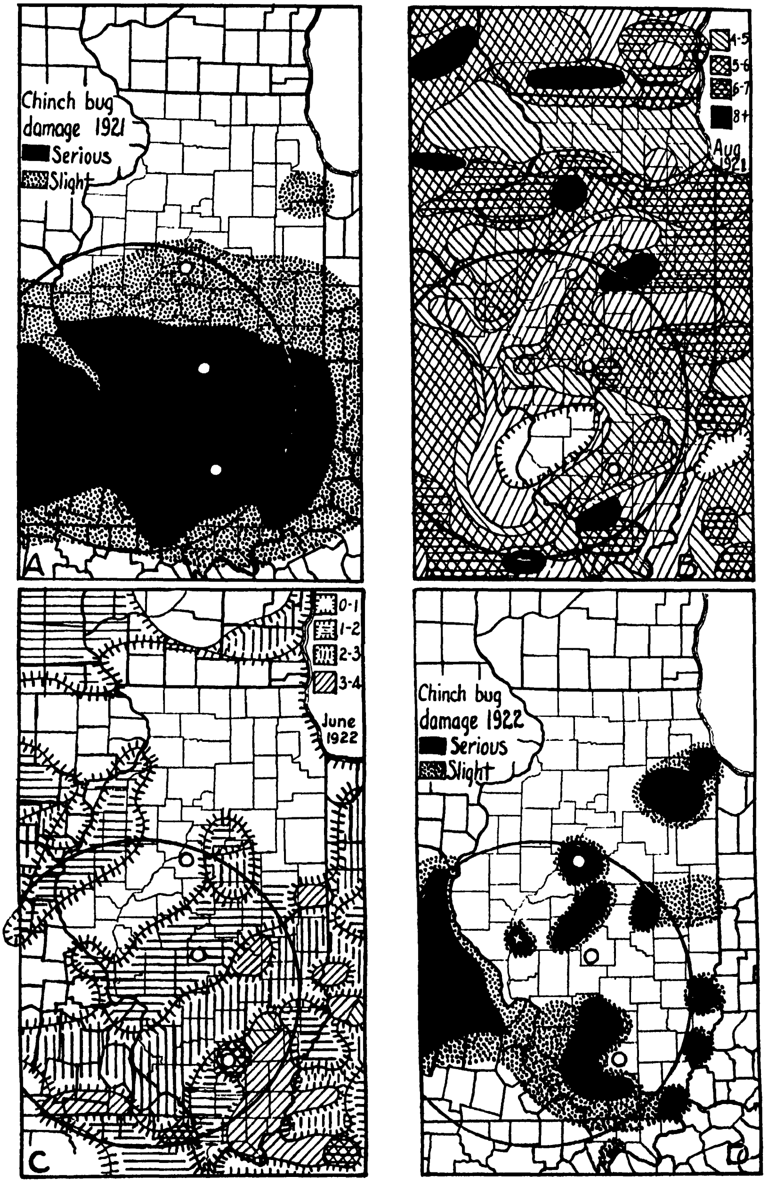

FIG. 7. Showing the relation of rainfall to chinch bug population in the summers of 1921 and 1922. For explanation, see text.

was possible under 4 to 5 inches of rain which was followed by still lower precipitation in September and October. The most northerly circle marks the location of an area of low rainfall in June, 1922 (fig. 7C), which was followed by severe damage in 1922. It is not easy, however, to understand why this area does not extend farther to the southwest and connect with the area marked X. A partial answer is to be found in the rainfall of May and September.

The center circle represents the Morrisville weather station where the heavy August rainfall is shown in the map. This was followed by heavy September rain and a very unfavorably, rainy May 1922. Similar conditions occurred east to the limits of the area and west in the area between Morrisville and the Mississippi River, both in September and May.

The large "C" shaped area of heavy infestation in southern Illinois shows the effect of the heavy June rainfall in the prevention of nearly all crop damage. (Compare Map C and D.) To the east of this area, September and May were both unfavorable to chinch bugs, over more than half of the area. Of the three areas of survival of heavy populations near the Wabash River, the two most northerly areas were in the regions of generally favorable rainfall but the most southerly is not explainable on the basis of wather records.

Interpretation of the Outbreaks in Illinois 1879 to 1940 from Thomas' Annual Viewpoint.—The outbreak beginning in 1881 was preceded by three warm, dry years and persisted through five wet years in scattered localities where weather conditions may have been favorable in critical months. The great outbreak of 1888 followed two dry years and was ended by unusually heavy May and June rainfall in 1889, which is not indicated in the annual figures.

The Illinois outbreaks of the '80's have long puzzled the writers because of the numerous apparent exceptions to usual rules. The spotted character of the damage of 1881 to 1888 was checked against the available weather records of counties in which the damage occurred, considering only May and June as favorable when the rainfall was below normal or unfavorable when considerably above normal or average. Some attention was also given to May and June temperatures and the temperature and rainfall in conditions in August and September.

1882: Weather at three-fifths of the stations favorable to bugs.
1883: Weather at three-fifths of the stations unfavorable to bugs.
1884: No records in the counties concerned.
1885: All records unfavorable in May and June.
1886: All records unfavorable in May and June.
1887: Eighteen out of 22 records for May and June (one or both) favorable. The rainfall in all southern Illinois counties was below normal for both of these months.
1888: 25 out of 39 records for these months were unfavorable. The months of August, September, and in some localities, October, also were dry in 1887.

Following 1889 the bugs recovered a population after two warm, dry years and persisted in numbers locally for a period of five years but shrank to inconsequential numbers in 1896 again, due to unusually heavy May and June rainfall. The absence of bug damage during the 12 years, 1897 to 1908 inclusive, was due to unfavorable rainfall in May and June in one or both months in most of the years so staggered that no two favorable years came together except in southern Illinois in 1905–1906. These two years were, in general, preceded by an unfavorable August and September. From 1909 to 1940 inclusive, there were continuous local large populations and at least one outbreak of a general extent in 1934.

The 1915 reduction of bugs is correlated with high annual rainfall in that year.

The rainfall in June and also in August was very heavy. In August of that year from seven to nine inches of rain fell in one period of about 28 days. Heavy May and June rainfall in 1924 reduced the population in most localities and succeeding several years of low population correlated with similar May and June conditions.

General and Reproductive Vigor of Bug Populations.—It is well known that bugs often come out of hibernation in a very weak condition. This was true at Coulterville in 1913 when the application of oil sprays was being tested. The results of these sprays were definitely effective, but it was later found that this was due to the condition of the insect as a shower or spray of water was equally effective.

Bugs brought into the laboratory from points south of Springfield, Illinois, in early June 1917 were weak (Shelford, '32). This was at the edge of an area of severe damage during that year. Other bugs brought in in May 1921 from fields adjacent to the University of Illinois campus, also were weak. (The area was one of slight damage, fig. 1, 1921.) There was exceptional reproductive vigor in 1919 in specimens from Christian County, Illinois, where the damage was moderately severe, and again in 1925 from the same general area (fig. 1, 1925) when it was the only spot with damage. Christian County is near the center of the northern edge of severe damage (fig. 1, 1919). These bugs were bred in the laboratory under several different conditions of light and temperature, including constant and variable temperatures and humidities. Bugs bred under all the different conditions showed a comparable degree of reproductive vigor or general weakness, indicating that the physiological condition in each case had been established before the bugs were placed in the experiments (Shelford, '32).

A comparison of the fall and winter weather conditions preceding the summer in which the physiological condition of the bugs was known has shown only one consistent difference and that a heavier rainfall in October–November in the years in which the bugs were strong the following summer. Such rainfall is known to be important in the breaking of dormancy and the success of the codling moth.

These variations in vigor were made evident in the nine years, 1917 to 1925 inclusive, in which the senior author maintained summer cultures of chinch bugs in climate stimulating apparatus providing two constant temperatures and from three to five variable temperatures with two degrees of moisture in each. In order to have the cultures continue, it was frequently necessary to start them more than once. The success and vigor of these insects differed greatly from year to year. Table III shows the number of experiments made, the number of results produced, and the number of times started with the average number of generations. The rating of the vigor was arrived at by the simple formula given in connection with the table. This gave the vigor rating shown in the last column and indicated in graph form (fig. 8). It will be noted that there was a rise in vigor from 1917 to 1920, a sudden drop and gradual rise from 1921 to 1925. This vigor was obviously determined previous to bringing the insects in from

TABLE III. *Reproductive vigor of chinch bugs in cultures started with individuals collected out-of-doors*

Year	No. of Expt.	No. of times started	Total no. of new adults per expt.	Maximum number of generations		Rating
				Adult	Nymphal	
1917	7	7	1.4	1	1	1.4
1918	5	5	3.0	1	2	3.0
1919	12	18	11.7	2	3	31.2
1920	8	8	9.0	2	3	18.0
1921	9	27	4.4	1	1	1.4
1922	9	17	8.6	1	1	4.5
1923	8	15	7.0	1	2	3.7
1924	6	8	28.0	2	2	42.0
1925	7	7	90.0	3	4	270.0

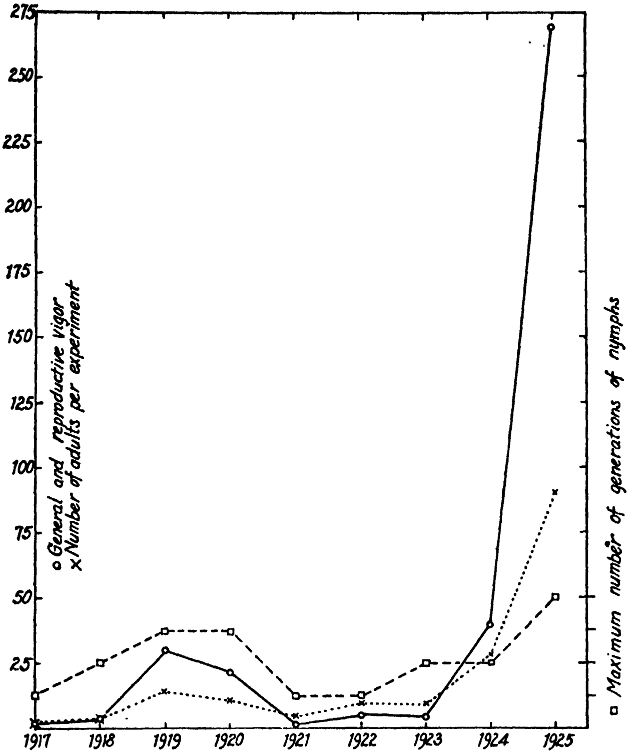

FIG. 8. Showing variation in vigor of bugs in cultures over a period of nine years. The vigor was manifested in all cultures. There were seven in all each year, differing strikingly in light, temperature, humidity and temperature and humidity variability.

the field and in vigorous years strong cultures grew up in all the various experimental conditions.

It is apparently not possible to ascribe this vigor to hormones. It may be the result of autumn and winter conditions. Possibly it may also be due in part to the presence or absence of certain fungus organisms on or in the bodies of the bugs. However, the sum total of this experience indicates that the physiological condition of the organism itself is an important factor that has to be considered in dealing with populations. The ratings in the sixth column are:

$$\frac{\text{No. of expt.}}{\text{No. of times started}}$$

× No. of new adults per expt.

× Max. No. of generations of adults.

1924 is 6/8 × 28 × 2 = 42.

The number of generations is not uniform for all experiments.

Population in Relation to Enemies.—The bird and mammal enemies of the chinch bug include song birds, quail, skunks, etc., but none of these takes enough bugs to materially influence populations. Webster ('07) rates the quail as an important enemy but investigators in Illinois have shown it to be much less important than Webster suggested.

The only insect enemy of the chinch bug of considerable importance is the small egg parasite, *Eumicrosoma benefica* Gahan, which sometimes destroys as much as 50 per cent of the chinch bug eggs. Of the predaceous insects, adults and nymphs of the gray damsel bug, *Reduviolus ferus* (L.): larvae of the *Chrysopa* (*C. illinoiensis* Banks) and

Hippodamia maculata Muls., and certain of the small ground beetles, particularly *Blechrus glabratus* Lec. and *B. pusio* Lec.: nymphs and adults of the bug (Nabid), *Pagasa fusca* (Stein), and the insidious plant bug, *Triphleps insidiosus* (Say), are the most important and most common. Some ground beetles feed on chinch bugs, but apparently not to any great extent. *Casnonia pennsylvanica* Linn., according to the observations made in Illinois, has been found to eat small numbers of bugs. A study such as that of Bàrnes ('42) on wheat midge, *Contarinia tritici* (Kby.), would be desirable. He measured the populations of both pest and parasite over a period of nine years.

GENERAL DISCUSSION

This will follow the chart, figure 9, which is made up from weather data from official sources, astronomical data from the publications of the International Astronomical Union and the chinch bug population in the 120,000 square mile territory. The two grades of damage recognized in the mapping shown in figure 1 were used to make up the curve of chinch bug population.

Transparent cross section was laid over maps much larger than those shown in figure 1. Each square (20 miles, 32 km., in diameter) covered 400 square miles, 1056 square kilometers. The number of squares in solid black repre-

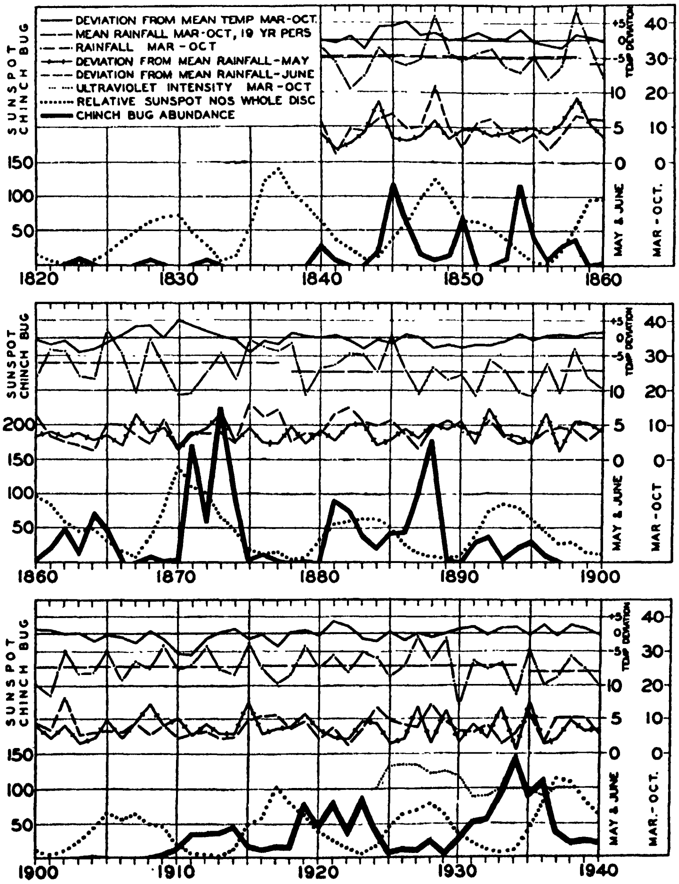

FIG. 9. Showing the rainfall, temperature and ultra-violet (available 15 years) data, 1840 to 1940, and sun spots and total bug population in the 120,000 square mile area of study, 1820 to 1940. For explanation, see text.

senting large damaging populations were counted likewise the squares representing slightly damaging populations were counted and divided by four, and the resulting figures added to the number of heavily populated 400 square mile (1056 square kilometer) areas. Records from 1820 to 1842 were regarded as 400 square mile units about three-fifths the size of a county. 1823, 1828, 1832 were regarded as one such unit, while 1840 was regarded as three units. Each was multiplied by ten to make them show on the graph and as a rough correction to take care of the small amount of land under cultivation. In records from 1843 through 1850 the values were multiplied by four: 1851 to 1860 by two. Thereafter, the actual values were used. The peaks of population are merely raised to a hypothetical value comparable with the later records. The heavy, black line represents the entire chinch bug population.

The chinch bug population curve then represents an evaluation of the entire population over an area large enough to eliminate the effect of local weather variations. Since 1860 especially, and for a period of more than 60 years, it also eliminates the missing of areas of high or low abundance due to scattered observation stations. To be sure, the estimates are of economic densities and no attempt has been made to correct the figures for differences in areas of favorable food plants in different areas and years. Furthermore, no attempt has been made to work out the astronomical figures which would result, e.g., from the presence of 17,000 bugs per m.^{2} on one-half the 90,000 square miles probably covered by heavily damaged food plants in 1873 (see fig. 1). The main objective at this point was to eliminate the effects of the spotty character, of weather, animal abundance and observation which have obscured the broader trends in most studies.

An examination of figure 9 indicates that there was a major outbreak in 1840 and other major outbreaks in 1853, 1858, 1863, 1873, 1881, 1888, etc.

Because of the recent discussion of sun spots in relation to grasshopper outbreaks and grouse abundance by Criddle ('30, '31, '32) and rabbit fluctuation by MacLullich ('36), a graph of sun spot numbers used in connection with studies of the snowshoe rabbit was transposed into the chinch bug population graph and extended through 1940. All data as to sunspot numbers are originally from the International Astronomical Union.

Ultra-violet light intensity as observed at the Mount Wilson Observatory, 1923–1938 is also plotted. The figures used are 100 times the ratio of ultraviolet (320 mu) to green (500 mu) (Pettit, '32). The intensity is greatest when sunspots are most numerous. This is shown by Pettit in considerable detail, applying from day to day and month to month, as well as to his averages. Clayton (1921, 1925, 1926) has published data showing correlation between solar radiation and atmospheric conditions.

DeLury of the Dominion Observatory, Ottawa (1936), pointed out the difference in weather response to numbers of sun spots in different geographical regions. He stated in that connection that at Edmonton, Alberta, at the period of few sun spots the rainfall may be 50 per cent greater than at the time of maximum, while at the same time, temperature may be as much as 4° F. higher than at the time of maximum. At coastal points such as St. John's, Newfoundland, rainfall is 20° higher at the time of maximum than at that of minimum. A comparison of figures 4 and 11 indicates that since 1860 temperatures were most often higher when sun spots were low, but there appears to be no fixed relation.

The rainfall for May and June for the entire State of Illinois is plotted separately for 1873 to 1940. Figures previous to 1872 are one-half the combined rainfall of St. Louis and Chicago. The rainfall for March through October is one-half the sum of Chicago and St. Louis rainfall. In connection with this the mean for 19 year periods is plotted in accord with Thomas' 1880 method. The annual rainfall shows a decline from the first of these periods, 1840 through 1858, a continued decline through the five 19-year periods ending with 1934, and an indication of continued decline during the first seven years of the seventh period (only six shown, see fig. 4). The season in which bugs may be active at least in some years, March to October inclusive, differs in that there is decline of almost 5.0 inches (12.7 cm.) between the first and third periods, a rise of 1.6 inches (4.06 cm.) between the third and fifth periods, and an indicated decline for the first seven years of the sixth period.

The temperature relations for the March through October period are indicated as deviation from an average annual mean. The figure for this is one-half the sum of the Chicago and St. Louis general mean, which is 62.7° F. (17.0° C.). The deviations are plotted in Fahrenheit degrees.

It becomes evident on inspection that the principal outbreaks have occurred in periods of low or medium sun spot numbers. There are some discrepancies and irregularities, but in every case the maximum sun spot numbers are found at a time of lowered population. In general, the highest populations fall during the increase and decline in sun spot numbers, although there is a suggestion of exceptions to this between 1910 and 1940.

An inspection of the sun spot maxima shows that they have been separated by periods of seven to fourteen years duration. While the average is 11.4 years, the use of such a figure for a period as short as 120 years is useless. A similar situation holds for chinch bug abundance. The small "cycles" range from two to eight years, with an average of 4.8 years. The large outbreaks are seven to thirteen years apart, with the average of 9.6 years. These two figures, 4.8 and 9.6, seem quite misleading and appear to the writers as tending to obscure rather than clarify the relations. The 1925 and 1930 small population appears to be correlated with high ultra-violet intensity.

In checking the abundance of bugs with variations in May and June rainfall the five inch line of figure 11 may be used as a base. Usually any rainfall as low as three inches is favorable to bugs, while more than four inches is unfavorable. As a rule, when either May or June is dry, there is an increase in population as indicated by damage done. The rainfall for the growing season taken with the deviation from normal temperature shows a good correlation between chinch bug abundance and low rainfall and high temperature in combination. The reverse is true also.

There are exceptions to this, however, because the general average does not give expression to critical periods; for example, the high temperature and low rainfall of the 1867 growing season was nullified by high May and very high June rainfall. The period 1896 to 1909 was characterized by very low chinch bug populations. The temperature was only about one degree Fahrenheit above normal. As a rule rainfall in *either* May *or* June was too high for the insects. There was a small local outbreak in Washington County, Illinois, in 1904. Both May and June were favorable in 1903. The late summer and autumn were also favorable, which gave opportunity for a population to build up. This was followed by a favorable May and June and slight damage to crops occurred, although the general temperature conditions were favorable. Weather stations in the surrounding counties indicated much less favorable weather. The period 1896 to 1908 was characterized in the main by high and low May and June rainfall alternating from year to year. With the exception noted above, there was, accordingly, no two successive years which would permit population build up.

In general, the abundance of the bugs is most closely correlated with May-June rainfall. If both months are dry, the weather is favorable. If either or both months have heavy rainfall, the weather is unfavorable. Explanations on a weather basis are never quite complete nor the variation in vigor explained. The difficulties with the weather data have been discussed earlier. The question of vigor demands breeding and physiological study which will probably have to be prolonged and expensive.

SUMMARY

1. Populations of chinch bugs vary in midsummer from very few (or even none in certain localities) to 70,000,000 per acre (175,000,000 per hectare) in others.

2. The study demonstrates that to make proper correlations with the broader aspects of meteorological conditions, closely placed observation stations are necessary so that the average condition over a large territory can be arrived at.

3. Records from 1820 to 1940 on an area of 120,000 square miles with its center near the center of Illinois, are presented (fig. 9). There is correlation with sun spot numbers, but the use of average time between sun spot maxima and population maxima are rejected as meaningless because of the variation in both. During one period in which both are available, the correlation of population with ultra-violet intensity is closer than with sun spot numbers.

4. Within this area of study the correlation of much, or little, May or June rainfall with few, or many, insects is good. But when rainfall in either month is high, a very large overwintering population is probably necessary to provide a chance for a population to pass or fail to reach the critical early nymphal period at the time the heavy rains come.

5. Rainfall considerably below normal in August, September, and October often gives rise to a large overwintering population following a small one. If the spring months are favorable, a population sufficiently large to cause crop damage may arise.

6. Populations sufficient to cause crop damages are associated with growing seasons (March through October) in which temperatures are above normal, rainfall below normal.

7. The monthly summation and averaging period of weather bureaus is two to four times too long for good biological use of weather data. Spottiness of rainfall indicates that weather stations in the area of study are about 20 times too far apart to provide data for such study.

8. There is an unexplained difference in the vigor of chinch bugs on emerging from hibernation in different years.

9. No explanation of the rises of populations is complete or perfect, but on the whole, correlation with weather conditions is very good.

ACKNOWLEDGMENTS

The writers are indebted to the entomologists of the adjoining states for assistance in evaluating the damage to crops in the portions of their states in our study area, as follows: Professor J. J. Davis, Indiana; Dr. E. L. Chambers, Wisconsin; Dr. C. J. Drake, Iowa; Dr. G. C. Decker, Iowa; Dr. L. Haseman, Missouri; Dr. M. L. Didlake, Kentucky, and Dr. P. Luginbill, U. S. Department of Agriculture (Indiana).

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SUNSCALD OF EASTERN WHITE PINE, *PINUS STROBUS* L.[1]

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Many eastern white pine trees (*Pinus strobus* L.) standing on the edge of cuttings often show dead strips of bark on their sun-exposed sides. In many cases the dead bark peels off, exposing the sapwood, or appears merely as a depressed discolored area. The injury apparently is seldom serious enough to kill the tree, but because of the exposed area and the formation of callus tissue on its edges, it seriously degrades logs. It may provide entrance to fungi and boring insects which can damage the rest of the tree and endanger the remainder of the stand. A similar injury called sunscald is well known in fruit orchards, especially on apple, peach, and cherry trees, and is thought to be traceable to the combined action of sun and low temperature during the winter.

It is difficult to estimate the extent of the damage from this injury in terms of board feet. However, injured trees have been observed throughout the white pine region of New England, and in plantations outside this region. Old-time operators in Maine and New Hampshire talk about "sun-scorch" as something that "always hits white pine left after cutting." This is a somewhat exaggerated picture of the importance of the injury because only trees immediately adjacent to the northern or eastern edge of cuttings or along roads are likely to be even susceptible to the injury. It seems probable that sunscalded trees comprise only a fraction of one per cent of the total number of white pines; in fact a figure of one in one thousand might be a more nearly correct guess than one in one hundred. The points to remember, however, are that where it occurs, the woodlot owner loses, and that injury is done to a high percentage of the stems under what appear to be ideal conditions for the occurrence of sunscald.

REVIEW OF LITERATURE

Symptoms of Sunscald on Forest Trees

The injury was listed as "frost spot" by Sorauer ('09), "bark scorching" by Fisher ('07) and Hartig ('92, '94), and as sunscald by Parsons ('89), Hartley and Hahn ('20), Schwarz ('32), McMahon ('39), and others.

Boyce ('36) summarized the present state of knowledge on sunscald by pointing out that when certain trees with smooth, thin bark are suddenly exposed to summer sun by removal of their neighbors, the bark may be killed and open wounds may result. The injury, known as "bark scorch" or sunscald, usually appears on the south or southwest sides of the trees on the basal portion of the trunk and is most common on trees which have been growing in dense stands. Overheating and drying out of the inner bark and cambium have been cited as a possible cause. The injury has been reported on beech, birch, maple, balsam fir, Douglas fir, eastern white pine, and spruce. Boyce also referred to "an exactly similar injury termed winter sunscald" which is said to be caused by a combination of high and low temperatures during the late winter or early spring. Heald ('26) said that winter sunscald is probably much more common on forest trees than summer sunscald.

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[1] A condensation of a dissertation presented to the faculty of the Graduate School of Yale University in candidacy for the degree of Doctor of Philosophy. This work was done under the direction of Professors R. C. Hawley, H. J. Lutz, and P. R. Burkholder. Grateful acknowledgment is made to these men, and to the staff members of the Northeastern Forest Experiment Station, especially to Lieutenant J. W. Duffield, Mary C. Weldon, Lieutenant C. R. Saxton, and Helen Wienhusen.

[2] Formerly maintained in cooperation with Yale University, New Haven, Connecticut.

Symptoms of Sunscald on Fruit Trees

Winter injury of fruit trees has been under investigation for some time. The apparent similarity of sunscald injury on fruit and forest trees deserves brief mention here. It is first necessary to rule out the type of injury described by Harvey ('25) and others as heat canker of fruit and vegetables, appearing as bacteriologically sterile, discolored spots ascribed to heat reflected from the soil. Sunscald proper, on fruit trees, was described by deJonghe ('56), Waite ('05), Bradford and Cardinell ('26), and others. Mix ('16) in a very detailed study of the injury indicated that sunscald affected the bark cambium and outer sapwood on the southwest side of the trunk; that it was probably a winter injury caused by freezing to death after the tissues had been warmed up by sunshine on bright cold winter days. Gardner, Bradford and Hooker ('22) noted that it was found on all types of fruit trees. Very small trees were rarely troubled by winter sunscald, and trees old enough to develop thick, scaly bark were not as subject in the parts so protected. The injury had a dead and dry appearance on the southwest side. The bark became loose and fell away exposing an area of dead sapwood. The immediate obvious effect was the partial obstruction of the movement of nutrient and food materials; more important was the exposure to fungi and boring insects and the mechanical weakening of the tree. They pointed out that summer sunscald might also occur, basing this largely on Hartig's records of lethal temperatures in Bavaria. Winter sunscald "is not induced by simple insolation but by interacting effects of heat and cold." Early writers attributed the injury to sudden thawing, to increased flow of sap followed by freezing so that the bark was pushed off, to breaking of dormancy of the warmed area, and to alternate freezing and thawing. Rapid freezing has serious effects, so serious, in fact, as to "seem adequate to explain killing by sunscald without any assumption that growth has started." Rapid freezing to − 20° C. has been found to be lethal, and slow freezing to − 28° C. has also been found to be fatal.

Normal Bark and Wood Development

According to Brown ('15), growth in white pine is of two types; that without cell division, and that with cell division. Beginning in the spring, early in March at Ithaca, New York, the phloem increased radially without cell division, by as much as 50 to 100 per cent. Later in the spring, about the last half of April at Ithaca, rapid growth by cell division began, and xylem elements were formed inside of the cambium, and at a slower rate phloem elements were formed outside the cambium. The formation of xylem elements, Brown noted, began first in the trunk below the apical shoot and spread both ways; for this reason growth at the base of the tree might start a few weeks after that in the crown. This is in close agreement with the careful work of Priestley ('30), and is partially confirmed by Kienholz ('34) in red and white pine at Keene, New Hampshire, and by related work of Abbe and Crafts ('39), and deZeeuw ('41).

Seasonal relation of cambial activity is of considerable importance in attempting to fix the time of occurrence of sunscald injury. Work along this line has been done by Buckhout ('07), and Chalk ('30), besides those already listed. To summarize this work, it would appear that geographic location, site, and weather may determine the time of inception of cambial activity in the spring, most commonly in early April. Complete cessation of cambial activity, in the case of white pine in northeastern United States, may occur by October 1.

Phloem differentiation proceeds in all temperatures except those far below freezing. The cells of phloem parenchyma rapidly vacuolate, become filled with dark-colored substances, expand and crush the resisting layers. The parenchyma contains starch and tannins in autumn and oil globules in winter. Later activity gives rise to cork cambiums to produce the phellem of the outer bark. This process of cork formation is stimulated by direct insolation.

Tree Temperatures

Sunscald has been observed by many investigators to occur principally on the south and southwest sides of trees, and therefore has been attributed to excessive heating of cambial layers by Hartig ('92, '94), Fisher ('07), and others after them. The findings of many early workers, Russell ('89), Squires ('95), Jones, Edson and Morse ('03), who used mercurial thermometers to measure cambial temperatures, must be questioned due to the heat capacity of such thermometers and the difficulty of inserting these instruments into the cambial region without producing injury. More recently Harvey ('19, '23), Baker ('29), Reynolds ('39), and others have used thermocouples to determine cambial temperatures. They have reported that temperatures on the south and west sides of trees may often be from 5° C. to 20° C. above those on the north sides. There are no records, beyond those of Hartig with mercury thermometers, indicating that summer temperatures of the cambial layer attain the high temperature level which is lethal for ordinary plant tissue.

The lethal high temperature for most plants lies in the neighborhood of 50° C. or above, but as Berkeley and Berkeley ('33), Shirley ('36), Bates and Roeser ('24), Baker ('29), and others have shown, a high temperature can be lethal if acting over a short time, whereas a lower temperature must act over a longer period to be lethal. Lorenz ('39), working on cortical parenchyma of white pine and other tree species, determined, by immersing naked tissue in a controlled-temperature water bath, that cells were killed when exposed for 30 minutes to temperatures of 57° C. and 59° C. but died in one minute at temperatures of 65° C. to 69° C. None were killed at 55° C. at exposures lasting 30 minutes. These values are of special interest in relation to Hartig's ('94) record of 55° C. (131° F.) between the wood and bark of a living 80-year-old spruce tree.

Theories of Temperature Effects

The literature on temperature effects is voluminous, contradictory and confusing. Fortunately several workers have already attempted to make sense out of confusion, and for the purposes of this condensation only mention is made of the monographs of Belehradek ('35) on temperature and living matter, and Levitt ('41) on low temperature effects. Both are recommended for careful study. The general conclusion from the studies reviewed by these two workers is that injury can occur from slow freezing if the temperature goes low enough, from rapid freezing, from rapid thawing in some cases, and possibly from repeated freezing and thawing.

OBSERVATIONS AND MEASUREMENTS

Observations on Injured Trees

The first step in this study was to determine the characteristics of trees showing injury from sunscald. The purpose was to discover the size, age, and position of trees most susceptible to injury, the nature and extent of the injury itself, and to obtain indications which might be helpful in avoiding damage from sunscald.

Search was made for injured trees in the Massabesic Experimental Forest at Alfred, Maine, and the nearby vicinity in York County; on and near the Caroline A. Fox State Forest at Hillsboro, New Hampshire; the vicinity of Peterboro, New Hampshire; the Yale Forest near Keene, New Hampshire; the Harvard Forest at Petersham, Massachusetts, and nearby areas; the Mt. Grace State Forest in Massachusetts; and the Maltby and Saltonstall tracts of the Eli Whitney

Forest of the New Haven Water Company in Connecticut. Some 147 such trees were found suitable for study (figure 1). On these injured trees the following measurements were made: diameter breast high, age, bark thickness of the uninjured part of the tree, crown class, the compass bearing, converted to azimuth, of the radius through the middle of the injured area, the height to the base and to the top of the injury, the maximum width of the injury, the diameter of the tree at the point of this maximum width, and the position of shade on the trunk at noon. In addition, descriptive notes were taken on bark color and condition, position of tree in the stand, and topography of the site.

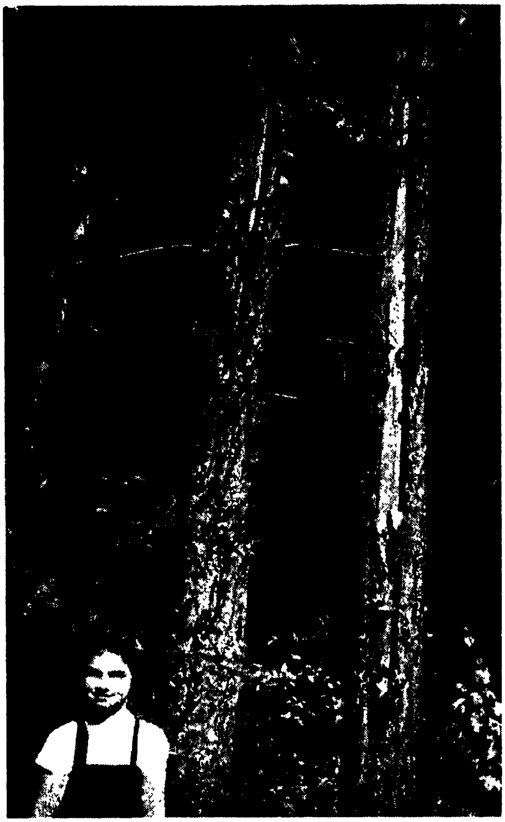

FIG. 1. Sunscalded trees on northeast side of opening in stand near East Waterboro, Maine. Note small stubs protruding from wound of tree at right.

Means and standard deviations were computed from these data to obtain a measure of the magnitude and the variability of each of the quantitative factors listed.

Cubes of bark and wood were chiselled from 15 trees growing in four localities. The cubes were taken so as to include injured wood, the callus, and healthy tissue for microscopic examinations. The material was placed in a killing solution made up of one part of glycerine to two parts of 70 per cent alcohol. Sections were cut on a sliding microtome, and temporary slides were prepared in lacto-phenol. Photomicrographs were made of the clearest sections.

Exposure Experiment

The position of injured trees in the stand and the direction of wounds on such trees, as noted in the observational phase of the study, suggested an experiment to test the effect of season of exposure and degree of shade on the direction and extent of sunscald injury.

A dense even-aged group of young natural white pine was selected on the Massabesic Experimental Forest at Alfred, Maine for the test. Twelve trees were chosen, four to be exposed in July, four in December, and the remaining four to be left as unexposed checks. On each of these twelve trees was arranged a series of three screens to provide 25 per cent, 50 per cent, and 75 per cent shade, and a segment of each trunk was left unscreened to permit full light. The screens used were similar to those employed by Mitchell ('36): 25 per cent shade was obtained by a screen of 4 × 4 mesh of wire 0.035 inch in diameter; 50 per cent shade by a screen of 18 × 18 mesh of wire 0.017 inch in diameter; and 75 per cent shade by a screen 70 × 70 mesh wire of 0.007 inch in diameter. The position of the various screens as well as the choice of treatment for the various trees was determined by random selection. The exposure for July and for December was secured by cutting all trees in a semicircle from east to south to west on a radius of at least 30 feet. This semicircular opening in the stand permitted the tree in question to receive uninterrupted sunlight in the summer from about 8:00 A.M. until about 4:30 P.M., and in the winter from about 9:00 A.M. until about 3:30 P.M. There were a few minor interferences from the shade of larger trees outside the semicircle, which it was impractical to remove. The screens on the trees, of course, faced this opening in each case. All twelve sets of screens were placed in July 1940. In October 1940, the four trees which had been exposed in the summer had the screens covered with burlap to prevent exposure to fluctuations in winter temperatures. Likewise, in April 1941, these burlap covers were removed and placed on the four trees which had been exposed in the winter to avoid exposure to changes in summer temperatures. These coverings and uncoverings were repeated in October 1941, and in April 1942.

Cambial Temperatures

Working on the assumption that the factors which affect cambial temperatures are the most important in sunscald, a test was designed to learn the effect on cambial temperature of season, time of day, degree of shade, and direction of exposure. Further, an effort was made to determine the relationship of cambial temperature to air temperature and solar radiation in summer and winter. To carry out this phase of the study preliminary tests were made in September 1940, over a period of a week. Details were worked out in these preliminary trials so that actual measurements could be made without difficulty in December 1940, January and February 1941, and July and August 1941.

Semicircular openings, similar to those described for the exposure experiment, were made in the plantation on the Maltby tract of the Eli Whitney Forest near New Haven, Connecticut. Screen arrangements similar to those in the exposure experiment were used. As shown in figure 2, under each shade condition on north, southeast, south, and southwest sides, thermocouples of iron and constantan were forced into the cambial region of the trees. These thermocouples were connected through lead-in wires to a switch box, which was connected to a portable indicating pyrometer. A recording hygrothermograph, and a current Centigrade thermometer were placed in a standard Weather Bureau instrument shelter. On the side of the shelter was nailed a wooden arm to support a pair of

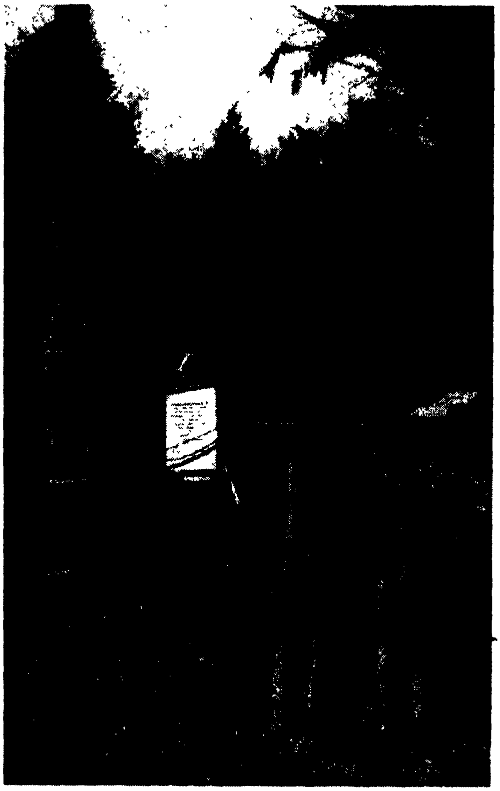

FIG. 2. Instrumental setup for measuring cambial temperatures, at Maltby, Connecticut. Thermocouples set into cambial region under each of four shade conditions, in order from top to bottom 25, 0, 50, and 75 per cent, on N, SE, S, and SW sides, are connected to switch box which is connected to pyrometer. Weston photoelectric cell on table. Instrument shelter in background supports black and white bulb thermometers, and contains hygrothermograph and current Centigrade thermometer.

current Centigrade thermometers, one with the bulb blackened with shellac and carbon black, the other whitened with thin flat white paint. These paired black and white thermometers, according to Hall ('32), are indicators of solar radiation. To supplement this measurement of solar radiation, a photoelectric illuminometer calibrated in foot-candles, was used. At half-hour intervals readings were made of cambial temperature under each of the four shade conditions and each of the four directions mentioned above; measurements of light intensity at the unshaded part of the tree for each of the four directions, of air temperature, and of black and white bulb temperature were also obtained.

These data were analyzed in two ways: by analysis of variance, and by regression analysis for summer and winter measurements separately.

DISCUSSION OF RESULTS

Characteristics of Trees Most Commonly Injured

An examination of table I indicates that the average injured tree is between 4 and 10 inches in diameter, is between 31 and 51 years of age, and has bark 3.7 to 7.5 millimeters thick. It is most likely in the intermediate crown class, although suppressed and codominant trees are often injured also. Severely pruned dominant trees in plantations have also been affected. The base of the wound begins from the ground line up to 8 feet from the ground and it may extend 3.5 to 23 feet up the trunk to heights of 6 to 29 feet. The wound varies from 3.3 to 7.3 inches in width at its widest point where the trunk diameter is apt to be 4.2 to 8.1 inches. The height of the lowest shade, determined largely by the tree's height or the height of its neighbors, when the sun is at or near the zenith, ranges from 5 to 32 feet, and this is always higher than the top of the wound. Shade from lesser vegetation greatly affects the height to the base of the wound, but this is extremely variable.

TABLE I. *Characteristics of injured trees*

	Mean	S. D.	Number of Observations
Diameter breast high (inches)	6.8	± 2.7	147
Age (years)	41.3	± 9.8	147
Bark thickness (mm.)	5.64	± 1.93	134
Compass direction (azimuth degrees) *	232.4	±40.98	143
Crown class			147
Suppressed	41	—	
Intermediate	66	—	
Codominant	33	—	
Dominant	7	—	
Height to base of wound (feet)	4.3	± 4.07	147
Height to top of wound (feet)	17.5	±11.67	147
Length of wound (feet)	13.4	± 9.84	147
Maximum width of wound (inches)	4.8	± 1.53	147
Diameter of tree at widest part of wound (inches)	6.2	± 1.96	140
Height of lowest shade on trunk between 10 A.M.–2 P.M. (feet)	18.8	±13.79	146

* Azimuth 0° = North; 90° = East; 135° = Southeast; 180° = South; 225° = Southwest; 270° = West.

Figure 3 shows that the injury most frequently occurs between the southwest and west-southwest direction on the trunk. This matter of direction is highly important because of its implications as to the manner of injury. Without exception the injured trees were exposed to the south quadrants, from east to west. No sunscald injury was found on trees exposed only to the north quadrants. This indicates that the injury is definitely related to sunshine. The southwest to west-southwest position of the injuries led to the study of actual cambial temperatures, the results of which are to be described later. Reasoning from the orientation of the injury alone, it would appear either that in the summer temperature was high enough to be lethal for the cambium, or that the winter sun raised the temperature just before sunset and the rapid temperature drop after sunset injured the tissue. More will be said of this later.

Topographic conditions of site did not appear to affect greatly the occurrence of sunscald injury. Among the 147 trees, many were on south and west slopes, but most were on level ground. Direction of exposure, as previously indicated, was

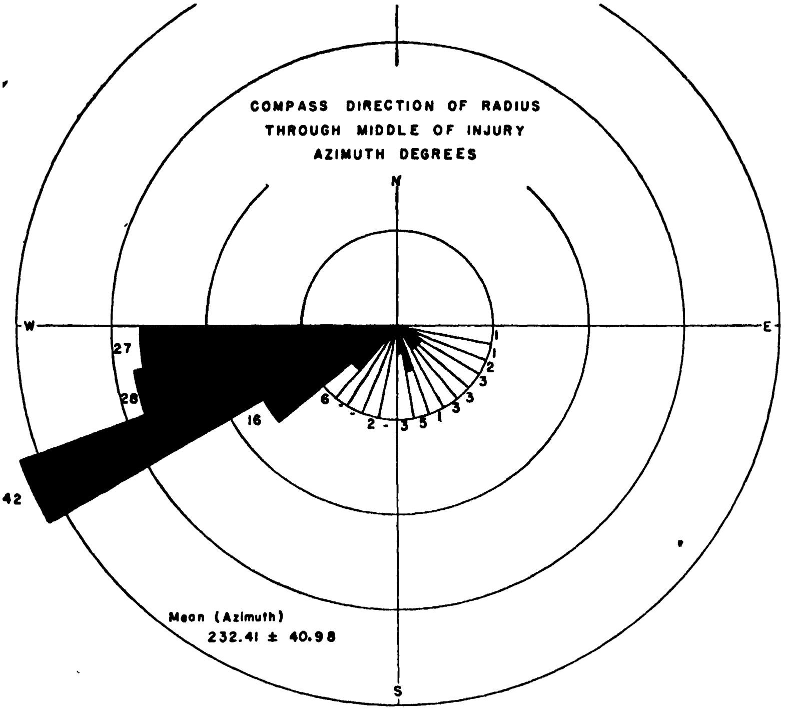

FIG. 3.

the most important factor, regardless of topography.

The wounded areas were invariably confined to those portions of the trunk where the bark was still smooth, unfissured, and without cork development. The uninjured side of the tree, near the wound, was usually greenish-black to brownish-black. In the case of the larger trees with rough bark near the base, the upper parts of the trunk where the bark was still smooth were injured.

A number of trees on the south and west edges of stands had been severely pruned, and many of these were badly sunscalded.

The injury itself was long and narrow, varying from a roughened, scorched appearance of the bark with slight injury to the cambium to small disconnected cracks which were callused over. There were extreme cases of exposure of the sapwood, grey to brown in color, with visible cracks from drying, and more or less well developed callused edges. In many cases small stubs of branches protruded from exposed wood, ruling out any possibility that the injury could have been caused by a falling tree. In numerous instances, emergence holes in the dead sapwood and galleries packed with shredded wood borings under the dead bark were evident. They were the work of the flatheaded apple-tree borer, *Chrysobothris femorata* (Oliv.).[3] The callus development, which was quite vigorous in many cases, caused the affected trunks to be so misshapen as to be worthless for logs. If the tree has succeeded in overgrowing the wound, the log when opened up will yield only low grade boards with pitch streaks and discolorations.

Microscopic study of sections taken from 15 wounded trees showed that at the region of the wound all tissues exterior to the xylem had been destroyed. In many cases there appeared to be an abundance of resin ducts in the uninjured portion of the rings near the wound. There was also a considerable pitchy accumulation under the callus edge where it overlay the wound surface.

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[3] Identified by Dr. Henry Bess, Division of Forest Insects, Bureau of Entomology and Plant Quarantine.

At the suggestion of Professor Robert Hess of Yale University, an effort was made to determine the season of injury. This was done by counting the rows of cells formed in the last annual ring from the previous year's last row of summer wood cells to the edge of the wound; and comparing this with similar counts made on the same annual ring on the uninjured part of the stem. A significant fact came out of this examination as illustrated in figure 4. In all 15 cases, the edge of the wound came at the last-laid summer wood cells, and the number of rows of cells in this annual ring at the wound, matched exactly the number of cells in this same ring on the healthy part of the tree. Referring to the work of Buckhout ('07), Brown ('15), and Kienholz ('34), it will be recalled that spring wood formation in white pine begins after April 1st, and summer wood formation ceases by October 1st. Apparently then, summer is not the time of occurrence of sunscald injury.

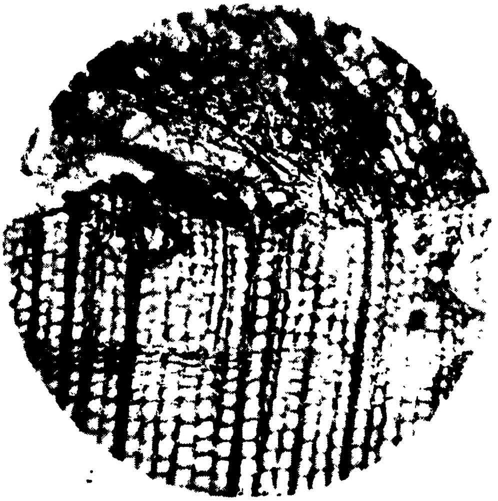


FIG. 4. Cross-section of wounded and healthy tissue of a sunscalded tree growing near Keene, New Hampshire. Note that just to the left of the resin duct there are 12 rows of cells in the last annual ring, ending with thick-walled summer wood cells. Well to the right of the duct in the uninjured portion there are also 12 rows of cells in the last annual ring. (Magnification is about 80 X.)

It is true that 15 is a small sample of the 147 injured trees, but the uniformity of the results from the four different localities should indicate that a 10 per cent sample was adequate.

The important points to remember thus far are: (1) the high frequency of occurrence of the injury on the southwest to west-southwest side of smooth-barked trees exposed on the south by opening up of the stand; (2) that the direction of the injury indicates that either a summer condition of high temperature (it must be 57° C. or higher according to Lorenz's results), or a winter condition of late afternoon temperature rise followed by a rapid temperature fall after sunset, may be the circumstances making possible sunscald injury; and (3) that the comparison of numbers of rows of cells in the last annual ring of wounded and healthy tissue proves that the injury cannot have occurred in the summer.

Exposure Experiment

As pointed out previously the exposure experiment, established on July 18, 1940, was designed to furnish information concerning the effect of season of exposure and degree of shade on direction and extent of sunscald injury. During the first 30 days following the exposure there were only two days when the air temperature at the headquarters weather station, about one-half mile away, reached 88° F., and only six days when it reached 85° F. This could therefore be classed as a normal summer. No injury appeared on the exposed trees.

The first frost occurred on October 17 and was followed by frosts on six nights within the following ten days. On December 4, the air temperature dropped to − 15° F. The December exposure was not made until two weeks later. Following exposure, on only one night did the temperature drop below 0° F. (January 14 it was − 4° F.). There were no sudden drops of temperature; the greatest was 30°, from 38° to 8° F. in 14 hours. This could consequently be considered a mild winter. No injury appeared on the exposed trees. The last frost occurred on April 23, 1941.

The summer of 1941 offered more promise than the previous summer, in that there were eight days with maximum air temperatures of 88° F. or higher; on two days the temperature reached 96° F., one day 95° F., two days 91° F., one day 90° F., and two days 88° F. Air temperatures such as these are somewhat above normal, but apparently not enough higher to cause sunscald injury to the exposed trees, for none has appeared as yet.

The only noticeable change occurred in the color of the bark of the summer-exposed trees at the fully exposed zone, and of the exposed part of all trunks, above the screens. The winter-exposed trees were protected from summer fluctuations by burlap over the screen frame. The exposed part of the trunk of these trees, above the screens, also showed discoloration. The dark blackish-green color, which seems to be normal, altered to a brownish or yellowish-green. The northern side of all trees remained blackish-green, and the unexposed check trees were not discolored. Examination of the cambial region beneath the discolored outer bark failed to show any injury. Similar discolorations can be seen on trees standing on the edges of blowdowns all through the hurricane-damaged area.

This seems to confirm the findings of deZeeuw ('41) that trees exposed to direct insolation tend to start deep cork formation earlier than shaded trees, and it is possible that the change in the chlorophyll-bearing tissue in the bark is one of the early stages of the process. Harvey ('23) gave a functional explanation of this color change by pointing out that reddish-brown bark absorbs less of the red end of the spectrum and thus protects the tissue beneath from heat injury. However this may be, the observable fact is that the bark is discolored, and tissue beneath it is uninjured. No sunscald has as yet occurred.

The summer of 1941 was extremely dry. The first frost in the fall of 1941 was a light one on the night of September 29, and this was followed by a heavy frost on October 25.

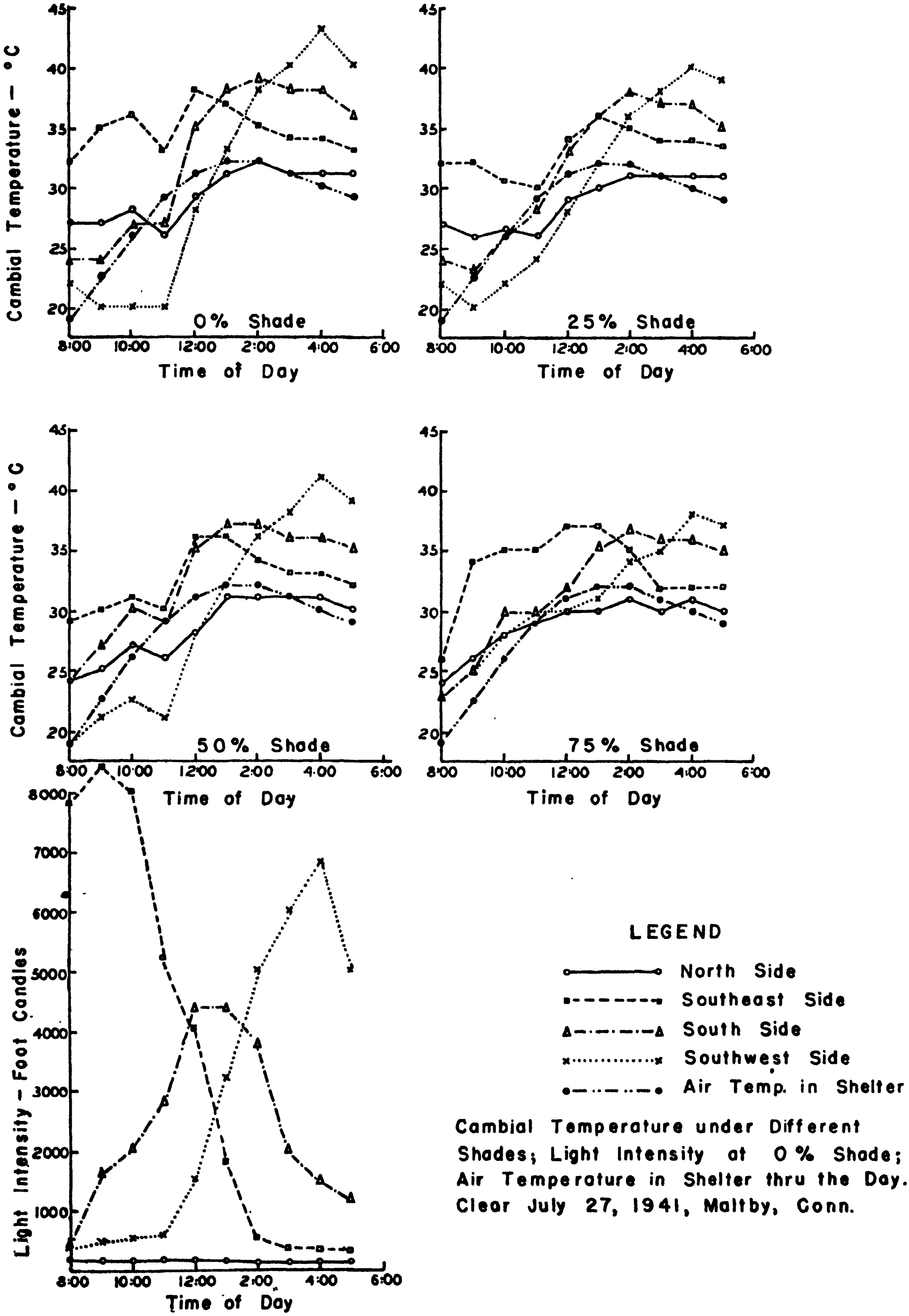
The winter of 1941 had a number of very cold days with temperatures down to − 14° F. and temperatures just above this on several successive days. There were frequent thaws, and much bright weather. At the time of the last examination, in the spring of 1942, no injury had appeared. Unfortunately circumstances connected with the war prevented further follow-up of this phase of the study.

Cambial Temperatures

Figures 5, 6, and 7 show cambial temperatures under different shade conditions, and sunlight intensities at the fully exposed zone of the tree at various hours of the day on different sides of the tree, for a clear July day, a clear February day, and a cloudy January day. Air temperatures taken in an instrument shelter at corresponding times are also shown.

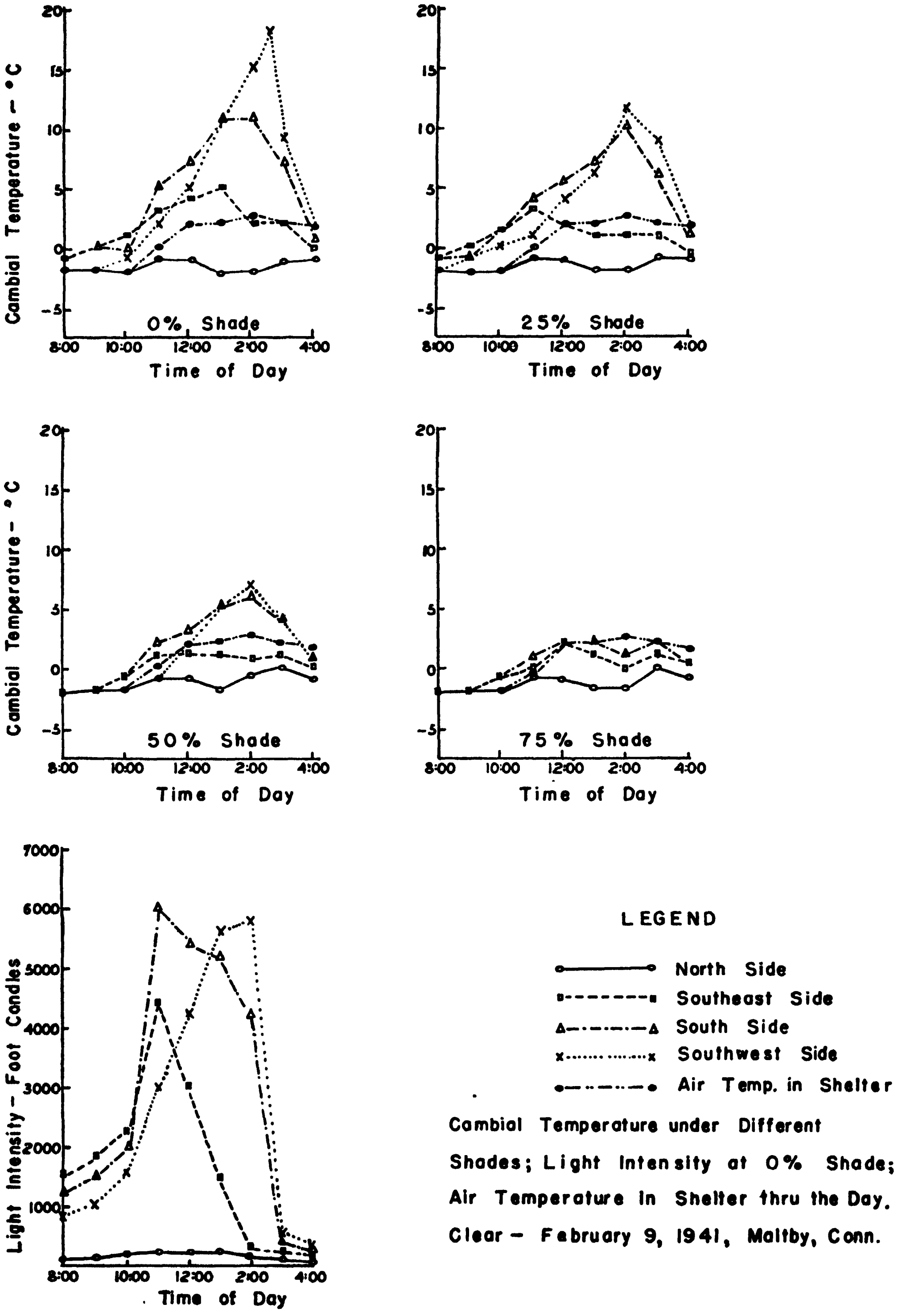
It is obvious that the temperature of a tree fluctuates during the day; that the temperature of different sides of a tree changes differently; that these differences are wider in the absence of shade than where shade is present; and that all these changes vary considerably with character of day, especially with air temperature and sunlight intensity.

Analyses of variance for the winter temperature emphasize these points. In both seasons it was found that character of day, degree of shade, direction of the sun, and time of day had a highly significant (statistical) influence on cambial temperatures. Also the character of



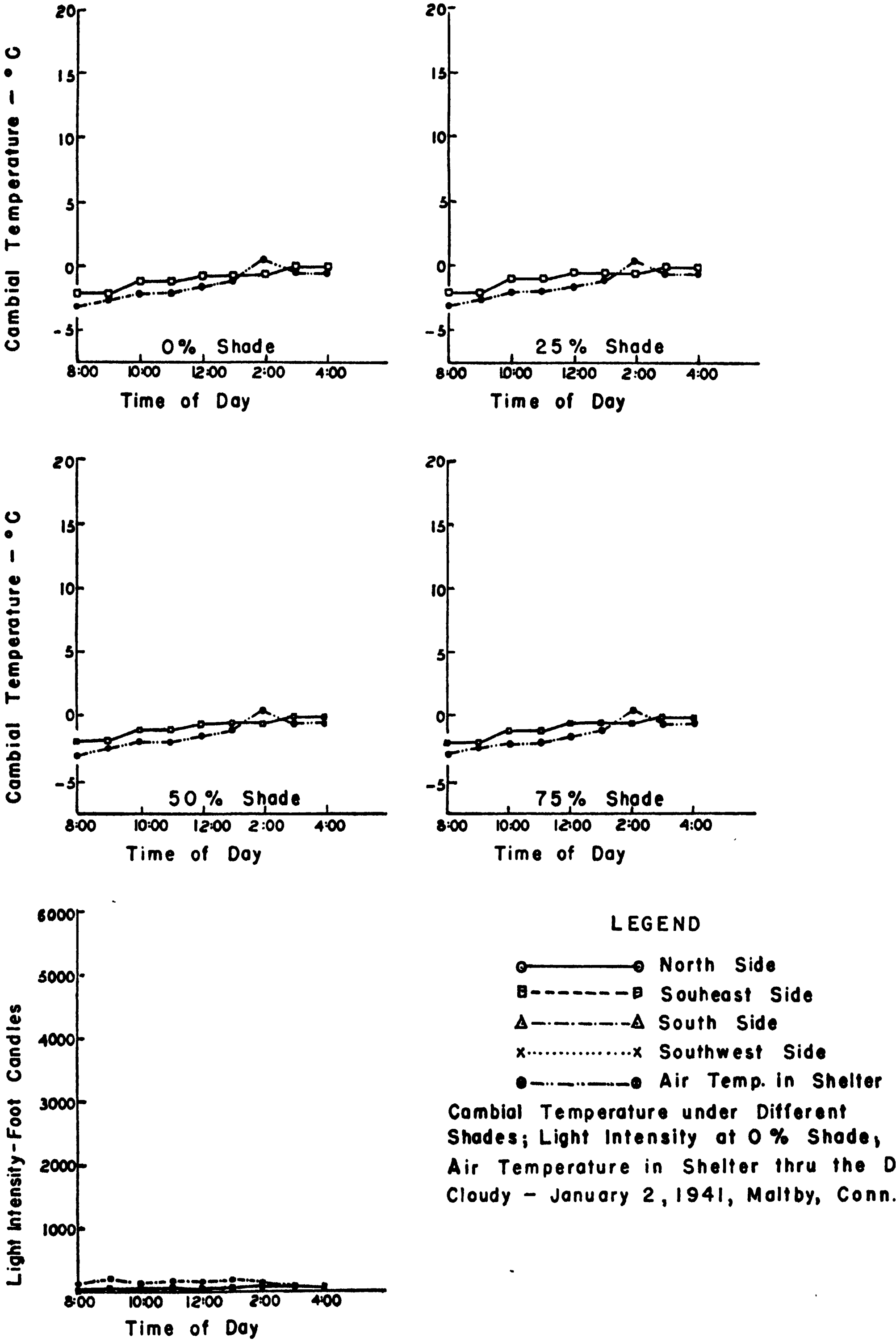
Cambial Temperature under Different Shades; Light Intensity at 0 % Shade; Air Temperature in Shelter thru the Day. Clear July 27, 1941, Maltby, Conn.

FIG. 5.



Cambial Temperature under Different Shades; Light Intensity at 0% Shade; Air Temperature in Shelter thru the Day. Clear – February 9, 1941, Maltby, Conn.

FIG. 6.



Cambial Temperature under Different Shades; Light Intensity at 0 % Shade, Air Temperature in Shelter thru the Day, Cloudy – January 2, 1941, Maltby, Conn.

FIG. 7.

day, that is the brightness or cloudiness of the day, significantly affected the influence of the shades, the direction of the sun, and the time of day on cambial temperatures. This is well shown in figure 7 for January 2, a cloudy day. The cloudiness reduced the differences in temperature between shades, caused the directional differences to disappear, and resulted in very little change through the hours of the day. The various degrees of shade, furthermore, had a significant effect on the influence of direction of the sun and hour of the day. For example, temperatures under 75 per cent shade varied less through the day and for the different directions than did those at the fully exposed zone. The effect of direction was significantly different at the various times through the day.

A more detailed study of figures 5, 6, and 7 shows that the temperature on the north side fluctuates less than that on the southeast, south, or southwest sides, and appears to follow air temperature more closely than on the other sides. This is understandable from the fact that the sun shines on the southeast, south, and southwest sides of the tree, but the north side is always shaded. In the summer the temperature on the north side is above air temperature through the night and until midmorning, then does not keep pace with change in air temperature until early in the afternoon when air temperature passes its peak; then north side temperature does not drop as rapidly as air temperature late in the afternoon.

Temperature on the southeast side rises most rapidly in the early part of the morning when sunlight is most intense on this part of the tree. This rise continues until about noon, when the cambial temperature on this side falls, before air temperature attains its maximum, as the sun strikes the southern and the southwestern sides of the tree. This is true for both summer and winter although the peak seems to be reached later in the day in winter than in summer. In the winter on cold days, the southeast side passes through the freezing point before the other sides, thaws out most rapidly on bright days, and does not pass back through the freezing point until sometime in the afternoon.

The temperature of the south side begins to rise later than that of the southeast side but rises more rapidly when once it starts, has a higher but flatter maximum, and in winter it drops more rapidly. In the winter it rises through the freezing point about midmorning, and is subject to considerable changes as clouds move across the sun, dropping back through the freezing point in the late afternoon on clear days.

The southwest side warms up more slowly than the southeast or south sides, but reaches a higher maximum late in the afternoon. The highest summer temperature recorded in these studies, 43° C., occurred on the southwest side at 4 P.M. This temperature is a full 12° C. below that reported by Hartig ('94), 14° C. below the lethal temperature determined by Lorenz ('39) in his laboratory study, and a few degrees higher than that recorded by Reynolds ('39). In the winter the temperature of the southwest side, after reaching its highest point in the middle to late afternoon, drops more rapidly than that of any other side when the sun falls below the neighboring trees.

Figures 5, 6, and 7, giving the light intensity, show that in the early morning the southeast side receives the strongest sunshine; that on the south side it increases in intensity more slowly, reaching a maximum about noon and remains at this maximum for an hour or more; that on the southwest it increases at an even slower rate, reaching a maximum in later afternoon, and drops sharply; while on the north side it remains uniformly low throughout the day.

The relation of maximum cambial temperatures at the fully exposed zone to air temperature, and maximum light intensity, was studied by regression analyses made separately for winter and for summer. These brought out the inevitable fact that cambial temperature is closely related to air temperature, especially on cloudy days. On bright days the differences in temperature between the sunny parts of the tree and the shady parts of the tree in relation to air temperature were marked.

The important point is that the maximum cambial temperatures (41° C. to 43° C.) recorded were maintained for such a short period, less than one-half hour, that they could not possibly have had any lethal effect. Shirley's study ('36) showed that exposure to such temperatures in a water bath for 5 hours failed to kill tops of seedlings. This would therefore indicate that high temperatures must be ruled out as the cause of sunscald, in New England at least.

APPLICATION IN SILVICULTURAL PRACTICE

The obvious lesson learned from this study is that sunscald injury can be avoided by maintaining shade on the west, southwest, or south sides of smooth-barked young trees.

To accomplish this, cuttings must never be so complete as to leave the south sides of trees exposed to winter sunshine. The southern and western borders of the forest should have low-branching trees as a protective screen for the remainder of the stand. Such screening trees should not be cut. Shelterwood cuttings, according to McMahon ('39), produce the minimum injury, presumably because the gradual opening of the stand by this method permits the early initiation of deep cork formation, as described by deZeeuw ('41), before complete exposure is accomplished; and practically all the larger trees are removed before complete exposure is necessary for the established reproduction.

McMahon ('39) also indicated that group selection cuttings result in more injury and clear-cutting in most injury on the north and east edges of the openings made. It should follow that if the openings are small enough to permit shading from the south (the width should be less than the height of the remaining trees), the injury could be reduced. This fits in well with sound silvicultural practice because openings of such width will permit effective seeding from the remaining trees.

Where clear-cutting in strips or groups wider than that recommended is inevitable, the direction of such strips should be confined to the northeast-southwest. This will permit the least exposure to late afternoon sun. Furthermore, in many parts of the white pine region of New England the prevailing wind direction about the time of seed fall in September and early October is from the northwest so that seeding should be most effective in such openings which permit the seed to blow across them.

Too-severe pruning, when done in one step in stands so open that there is shade neither from the tree's own crown nor from the crown of neighboring trees, may be especially serious, because pruning is ordinarily done on trees at an age when the bark is smooth, dark green, and tender. Pruning should be done in two or more steps so that the exposure will not be too sudden.

Good silvicultural practices need not be modified to prevent sunscald injury in most cases, because such practices ordinarily result in good protection to the reserve stand and to selected crop trees.

SUMMARY AND CONCLUSIONS

1. Sunscald is a serious injury to the cambium on the southwest side of the trunks of trees, revealing itself as dead strips of bark, which partially peel off and expose the killed sapwood. This wounding renders unmerchantable, or seriously degrades, logs cut from the affected part of the tree, and offers entrance to insects and diseases which may cause further deterioration of the tree and endanger the remainder of the stand.

2. The injury occurs on dark-colored smooth-barked trees on the north and

east edges of openings made in forest stands. The average characteristics of white pine trees most subject to sunscald are as follows: Diameter—4 to 10 inches, age—31 to 51 years, crown class intermediate, and a bark thickness of 3.7 to 7.5 millimeters. The injury itself has the following average dimensions: Length—6 to 29 feet, beginning at from 0 to 8 feet from the ground line, and extending 3.5 to 23 feet up the trunk; width—3.3 to 7.3 inches across at its widest part, usually where the diameter of the trunk is 4.2 to 8.1 inches. The height of the lowest shade when the sun is at or near the zenith is 5 to 32 feet on the trunk.

3. The occurrence of the wound most frequently on the west-southwest side of the tree indicates either that late afternoon summer temperatures were high enough to be lethal for the cambium, or that winter temperatures in late afternoon were such as to cause rapid drop after sunset.

4. Topography of the site did not materially influence the occurrence of the injury.

5. Microscopic examination of wounded tissue and of the neighboring healthy tissue showed that the edge of the wound came at the last-laid summer wood cells. The number of cell rows in this last annual ring at the wound matched exactly the number of cells in this same ring in the healthy tissue. The obvious interpretation is that the injury occurred after summer wood formation had stopped, and before spring wood formation had started. This would place the time of injury between October 1 and April 1, ruling out the possibility of summer injury.

6. Measurements were made of cambial temperatures in summer and winter. Character of day with regard to brightness or cloudiness, degree of shade, direction of the sun, and time of day significantly affected cambial temperatures. Each of these factors also significantly affected each of the other factors in their influence on cambial temperatures. These effects were brought out in analyses of variance.

7. Temperatures on the north side of the tree fluctuate less than those on the other sides. Temperatures on the southeast side rise most rapidly in the morning and begin to fall about noon; those on the south side rise more slowly, remain longer near their maximum, before falling about midafternoon; the temperatures of the southwest side take longest to rise, reach a higher maximum, and then drop most rapidly after the sun descends below the neighboring trees.

The highest summer temperature recorded (43° C.) occurred on the southwest side of the tree at 4 P.M. This is 14° C. below the lethal temperature recorded by Lorenz ('39). This temperature was maintained for such a short period, less than 30 minutes, that it could not possibly have had any lethal effect. Previous studies have shown that exposure to higher temperatures in a water bath for as long as 5 hours failed to kill plant tissue. High summer temperatures must therefore be ruled out as the cause of sunscald in New England. Most rapid thawing occurs on the southeast side; most frequent repeated thawing and freezing is encountered on the south side; and the most abrupt temperature drop is on the southwest side in winter.

8. Regression analyses brought out the inevitable fact that air temperature is the most important factor influencing changes in cambial temperature.

9. Sunscald in the Northeast appears to be a winter injury and the background from the literature, and evidence from the present study appear to point to rapid freezing as a possible cause.

10. Sunscald can be avoided by making the smallest possible openings consistent with sound silviculture, in harvest and improvement cuttings. "Screen" trees should be left uncut on the southern and western borders of woodlots. Extensive clear-cutting should not be used. Pruning of young trees should be done in two or more steps.

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THE ABUNDANCE OF THE COLLARED LEMMING (*DICROSTONYX GROENLANDICUS* (TR.) VAR. *RICHARDSONI* MER.)[1] IN THE CHURCHILL AREA, 1929 TO 1940

V. E. Shelford

Introduction

Many articles have been written on the abundance of northern animals but very little research to that end has been carried on in North America by scientific observers in the field. With the moving of the Canadian grain port from Port Nelson to Churchill in 1928–29 and the opening of the Hudson Bay Railway into Churchill in 1931, areas of northern tundra and its associated animals were made accessible. Churchill is only a 36-hour ride from The Pas, where previously as many days were necessary (Preble, '02). It was thought that it would be possible to correlate the abundance of animals in the local tundra areas near Churchill with the observations made by the weather station at hand.

During a study of the bioecology of the Churchill area in 1931 (Shelford and Twomey, '41), inquiries among trappers indicated that collared lemming (*Dicrostonyx*) had been very abundant in 1929 (less abundant in 1928) and scarce in 1930. A small amount of trapping for mice and lemmings was done in 1931. This trapping and the digging method recommended by Preble, revealed no lemmings, and no fresh signs were found. This condition offered an opportunity to trace the increase of the lemmings and mice (*Microtus drummondi* A and B) in connection with weather conditions. There were some amateur naturalists among the government and construction engineers. Ornithologists were doing work in the area annually which increased the likelihood of securing reports on the rodents in later years. Thus the reports of naturalists and trappers are included in this discussion along with more exact work by the writer and A. C. Twomey covering 1931, 1932, 1933, 1934, 1936, and 1939.

A grant from the National Research Council assisted the writer in returning in 1932 to make further observation on the rodents, especially the abundance of lemmings. For the necessary trapping, an area of low tundra from 1/4 mile to 1 mile from the Churchill town site was chosen because it was the area of the 1928, 1929, and 1930 observation of amateur naturalists and the route regularly traversed by the bird naturalists on their way to the lakes, sand ridges, and sparcely wooded areas to the south.

The collared lemming is the principal American species falling under this common name. Sixty-five miles north of Churchill, Preble found *Lemmus trimucronatus* Rich., but this species does not enter into the present discussion. *Lemmus* is smaller than *Dicrostonyx; Microtus* is very commonly confused with the lemming by trappers especially those from Europe, due perhaps to the superficial resemblance between the Norwegian lemming and the large species of *Microtus* which occupy the tundra. The collared lemming, *Dicrostonyx*, of the eastern North American Arctic on the west side of Hudson Bay and in Greenland is *Dicrostonyx groenlandicus* (Tr.) var. *richardsoni* Mer. On the east side of Hudson Bay along Hudson Straits, and the Atlantic side of the Quebec Peninsula, *D. hudsonicus* is understood to occur. The nomenclature used here is that credited to Hegerbol ('35), and adopted by the Bureau of Animal Population organized by Chitty and Elton ('37) for the work of the Canadian Arctic Wild Life Inquiry. This study included the lemming not distinguished as to genus and not clearly separated from Microtus. The work has, however, proved to be an important check on our local observations and on the observation of I. H. Smith and other trappers working between Tavane and Churchill.

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[1] The Churchill lemming was identified as *Dicrostonyx rubricatus richardsoni* at the U. S. National Museum (1933) but *D. hudso-* was used by Shelford and Twomey ('41), due to a clerical error in entering the name in Table 2, p. 55. *Groenlandicus* has now displaced *rubricatus*.

LIFE HISTORY AND HABITS OF DICROSTONYX

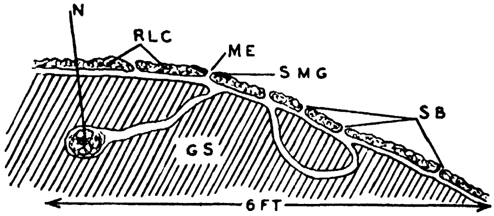
Breeding.—The lemming turns white in winter and is active all the year around. The winter elevator watchmen at Churchill stated that one entered their cabin one evening in midwinter. The evidence available, however, indicates that breeding is suspended from October to June or July. The first young have been recorded about July 1. The relation of litter size to population increases and declines is illuminated only by fragmentary evidence. Preble reported a female nursing three young and carrying three embryos on Aug. 12, 1900, about 100 miles north of Churchill. At Churchill (1900) lemming were fairly abundant and 80 were taken between July 23 and July 30, principally south of the river in our area of study where three young were the usual number. Jackson's ('26) graph of lemming abundance indicates a population decline from 1896 to 1901. The basis of the graph is not clear and the indicated decline lasted longer than any we observed.

On July 12, 1932, the first year of an increase, six young were found by the writer in the nest of one female, about 1/2 mile south of Churchill. Five to eight were reported by Twomey for the 1933, year of maximum, and four to six for 1936, another year of abundance.

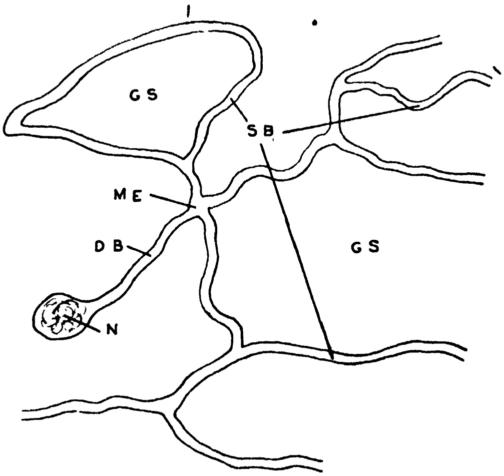
It is probable that the number of young in a litter may reach six during the increase, drop to four or five at the maximum, and to three during the decline in population.

Collett ('95) noted a remarkably short time between litters in Lemmus (Myopus) while the peak population is being built up. However, nothing is known about this condition in Dicrostonyx.

Burrows (fig. 1).—The habits of the lemming are simple. Figure 1 shows the form of a burrow in sandy soil where the animals extend over considerable area. On moist ground where they are confined to hummocks, the burrows are much less extensive but similar as regards the nest and several entrances. Fresh lemming burrows and other signs are easily recognized and lemmings are commonly out during the day so the number seen during several weeks constitutes a rough index of abundance.



CROSS SECTION OF LEMMING BURROW



SURFACE VIEW OF LEMMING BURROW

FIG. 1. Surface and sectional views of a lemming burrow. N—nest with young; M.E.—main entrance; S.M.G.—mound of gravel thrown out in digging; S.B.—surface burrow; G.S.—gravel and sand; D.B.—deep burrow. The dark surface shading in the upper figure is the vegetation mat. Excavated and sketched by A. C. Twomey.

Food.—The lemming feeds on almost any green material. Much can be learned from the fragments commonly dropped near the mouth of the burrows. Willow catkins, portions of cotton grass, and pieces of sedge were recorded. Twomey examined stomach contents of several lemming and found roots of grasses and the tender parts of "mosses." In winter their food probably remains the same but is sought under snow when snow is present. No depletion of food supply was noted by Twomey in the years of maximum abundance.

Enemies.—The avian enemies of the lemming are the snowy owl, rough legged-hawk, and short-eared owl. There is positive evidence that these three birds are very important in reducing the numbers of mice and lemmings. Twomey, who contributed to this study, was at Churchill in 1931, 1932, 1933, and 1936. He reported that short-eared and snowy owls were few in 1931 and 1932. In 1933, a year of lemming abundance, these two owls were more abundant, and in this year for the first time he found rough-legged hawks breeding. Twomey reported that lemmings were also abundant on Cape Churchill in the same year and numerous snowy owls and rough-legged hawks were associated with them there.

Twelve owl pellets picked up by the writer in 1934 showed remains of nine lemming and fifteen Microtus. Most pellets contained one lemming and one or two mouse remains. In the same year, Miss Theodora Cope saw no snowy owls (lemming minimum; June through August). According to local observers, the owls left early in the spring. There were few or no lemming reported in 1935 and no mention of owls.

In 1936 Twomey found the lemmings on sandy ridges and very abundant in the later part of the summer. There was a snowy owl's nest on every two linear miles of sandy ridge. Pellets showed that lemming and mice made up most of their diet. F. L. Farley reported ten nests of rough-legged hawks in 1936. He found no hawks in 1937 and 1938 and few or no owls in either 1937 or 1938 when lemmings were relatively few. Correspondents mentioned birds of prey as numerous in the last part of 1940 and 1941. All the reports from ornithologists and trappers indicate that birds take very many lemmings and mice.

According to Smith and others, weasels may also be credited with killing many lemmings and mice. Microtus makes ball nests of grass or grasslike material under the snow; in winter these may be quite numerous when mice are abundant. Loose materials other than grass may be incorporated especially in the outside layer. One mouse nest picked up in 1934 contained eleven Microtus tails, pieces of mouse skin and portions of crushed mouse skulls in the outer layers. These were all found within a short distance from a dwarf spruce which had evidently been the home of a weasel for a time. Strips of skin and skull fragments were common in nest balls; some were found elsewhere and still others reported by Miss Heidweyler. The writer found two dead mice in one nest ball. Persien stated that the lemmings sometimes make much larger balls than Microtus, but this has not been verified.

Foxes, wolves, and wolverines take many lemmings and caribou kill many chiefly by trampling them. The number of foxes is usually thought to be correlated with the abundance of lemmings.

Relations to Competing Species.—Mice of the genus Microtus occur with the lemming but do not require such large areas of good cover and tend to occur in grassy marshes to a greater extent than the lemming. At Churchill the population minima of *Microtus drummondi* and the lemming occur at about the same time but the maxima differ somewhat. The Microtus maximum came in 1932 and the lemming maximum in 1933. In 1932 four times as many mice as lemming were caught in traps on the same area (two hectare areas). In 1933 mice were scarce and lemming at a maximum. In 1931 and 1934 both species were at a minimum. In 1936 mice were abundant in early spring and summer at Churchill and north of Churchill during the winter of 1936–37.

The observations indicate that mice reach a maximum during the first of the two years of lemming increase. I. H. Smith reported an abundance of "shrews" in 1933 and 1940 and of a long-tailed mouse in 1941. Since the observations of the Canadian Arctic Wild Life Enquiry include mice and lemmings taken together, the tendency is probably to prolong the periods of "maxima."

Relations to Surface Water and Ice.—The collared lemming is not afraid of water and will dash or swim through pools in the low tundra. Correspondent I. H. Smith reports having seen their tracks on ice in the large northern lakes several miles from shore and also on the anchor and pressure ridge ice of Hudson Bay. Chitty and Chitty ('41) report mortality resulting from migration onto ice. Migration of the collared lemming is referred to occasionally but nothing definite is reported.

The local distribution of lemmings as regards the dryer and wetter portions of the tundra may lead to the spotty distribution often reported. They are most abundant on low ground following periods of low rainfall and on well drained soils following periods of heavy rainfall.

The Lemming Annual Cycle in Relation to Weather and Trapper Reports.—Knowledge of the life history is incomplete but at Churchill the first young are born very early in July following matings in June. The chief period of increase is probably the summer just as in the case of the European lemming (Collett, '95). Declines occur principally during the winter months.

Observations of trappers probably make up the greater part of the original information supplied for the Canadian Arctic Wild Life Inquiry. Trappers usually go to some of the small centers of population during June to dispose of their furs, secure supplies, etc. They return to their trapping grounds in late summer and early autumn. They thus see the lemming at their maximum and during the winter. Reports the Wild Life Enquiry made as of May 31 are thus concerned mainly with the reproduction of the summer of the preceding year as seen in autumn and winter. As compared with the weather conditions the reports are, in a sense, one year late.

The winter period if sufficiently unfavorable may result in the reduction of a population from a maximum to a minimum. When favorable, the winter appears to be the period of physiological conditioning of the animals for a high reproductive capacity during the following summer. Accordingly, the year, September through August, is used in the analysis of weather conditions. The weather conditions at meterological stations along the west shore of Hudson Bay and (two) in Hudson Strait have been analyzed.

Magnitude of Population Changes (fig. 2).—At the time of the low minima, fresh lemming signs are observed between one and four miles (1 to 4 mi. or 2 to 6 km.) apart. This was worked out in 1939 by 22 persons, scouting over about five square miles of good lemming territory within four miles of the Churchill townsite. With the population so scattered, it is difficult to make estimates and the animals are probably more numerous than observed. The author with one helper in 1934 and with two helpers in 1931 found no fresh lemming signs at all. It happened that several ornithologists and other naturalists tramped over the area within four miles (6 km.) of Churchill during the years of minima 1931, 1934, 1935, and 1939. Their reports were as follows:

In 1931, Twomey saw two lemmings in the season from June 1 to August 1; in 1934, one of three ornithologists saw one lemming; in 1935, one naturalist was the

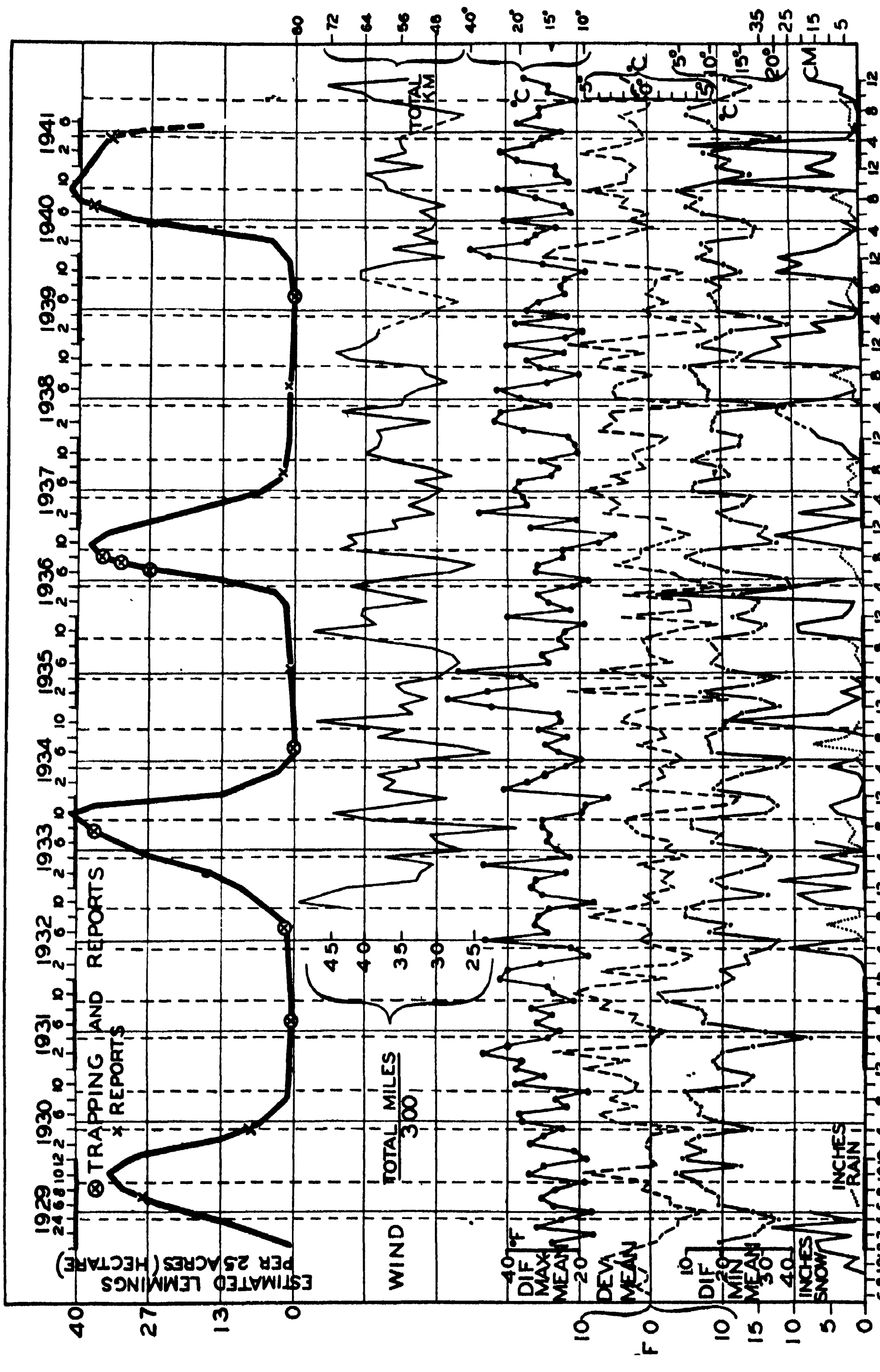

ESTIMATED LEMMINGS PER 25 ACRES (HECTARE)
40
27
13
0
⊗ TRAPPING AND REPORTS
× REPORTS
1929
1930
1931
1932
1933
1934
1935
1936
1937
1938
1939
1940
1941
WIND
TOTAL MILES 300
45
40
35
30
25
TOTAL KM
80
72
64
56
48
DIF MAX MEAN
°F
40
20
°C
40°
20°
15°
10°
DEVA MEAN
F 0
10
DIF MIN MEAN
15
20
30
40
5°
10°
15°
20°
INCHES SNOW
INCHES RAIN
CM
35
25
15
5
0

Fig. 2.

"only person at Churchill to see a lemming"; in 1939 two lemmings were seen.

FIG. 2. The upper curve represents the changes in lemming abundance from 1929 through 1941 in the area from Cape Churchill to Tavane. This curve is a rough expression of experience with the lemming rather than an accurate year to year determination by sampling, but based primarily on trapping. The X's indicate reports based on numbers seen. Trapping and digging were carried out at Churchill on the dates indicated by the X's in circles. The estimate of 42 lemmings per hectare for the beginning of winter is placed somewhat higher than the number established from the trapping in the middle of July.

The critical months, September to April inclusive, are marked off by vertical broken lines (Nov.–Apr. most important). The topmost weather curve is a record of wind velocity. Three curves in the center of the group are concerned with temperature while the bottom curves cover snowfall and precipitation.

There is no consistent correlation between lemming population and wind velocity though wind velocity may localize snow protection and increase winter dangers locally. In the curve at hand, the relatively low velocity through 1940–41 probably was favorable at Churchill, though low velocity did not prevail throughout the area in which the increases reported by Chitty and Chitty occurred.

The curves showing deviation of the maximum and of the minimum temperature from the *mean* or monthly normal for the month over a period of years, are placed above and below the deviation from the monthly mean. An inspection of the maxima for the critical months shows that the large deviation of maxima fall in the cold part of the year. These maxima may be significant in late spring because the melting of snow may possibly cause flooding of burrows and drowning of lemmings. Temperature maxima do not appear as significant as might be expected; they follow the general trend of the mean but with the largest differences showing no definite relation to rodent abundance.

The deviation from mean shows significant relations to lemming abundance when considered together with snowfall. Plus deviations or small negative ones accompanied by a good snowfall in each month characterized as critical, precede the three large increases. The deviations of minima follow quite closely, the deviation from normal. Their significance with reference to lemmings is clearly related to snowfall. The 1940–41 large population is correlated with warm weather and heavy snowfall. The relations are shown better by climographs (fig. 3). It must be borne in mind that two years favorable for increase are necessary to build up to a peak.

The distance between burrows and the trapping and digging data may be used to estimate population. Twomey made estimates for 1931, 1932, and 1933 based on counts of lemming seen during the summer (table I). It would take three generations of large litters to increase the population 100 fold as Twomey suggests and the frequency of burrows would make the numbers appear smaller than his estimates. The right half of the table shows the final estimate.

TABLE I. *The magnitude of population fluctuation*

Twomey's counts June 1 to Aug. 1 (approximately)	Estimate on basis of frequency of signs and trapping, per 100 hectares or 250 acres
1931......2 lemmings	Minimum............6 or 7
1932....200 lemmings	First year of increase........200
1933.20,000 lemmings	Maximum (at end of 2nd yr.).4,000

Six or seven lemmings per 100 hectares (250 acres) would be 200 to 450 meters apart. A thirty fold increase in the second year would give 200 lemmings per 100 hectares which would be about 70 meters apart. This is in accord with the actual findings in 1932. A twenty fold increase in the third year would give 4000 lemmings on the same area and these would be approximately 15 meters apart which is in accord with the frequency of old burrows in 1934, following a large population. In every case these figures would apply only to areas suited to the burrowing habits of the lemming.

The survival during the increase from 7 to 200 is far greater than when numbers are greater because our observations show that migratory avian enemies are not yet present in abundance.

RELATION TO WEATHER

Relation to Rainfall, Snowfall, and Temperature (fig. 2).—While the records of both weather and lemming abundance are known for too short a period to justify final conclusion, the suggestions growing out of analysis of available data are essential to correct future observations. The studies to date point to tentative conclusions such as are stated

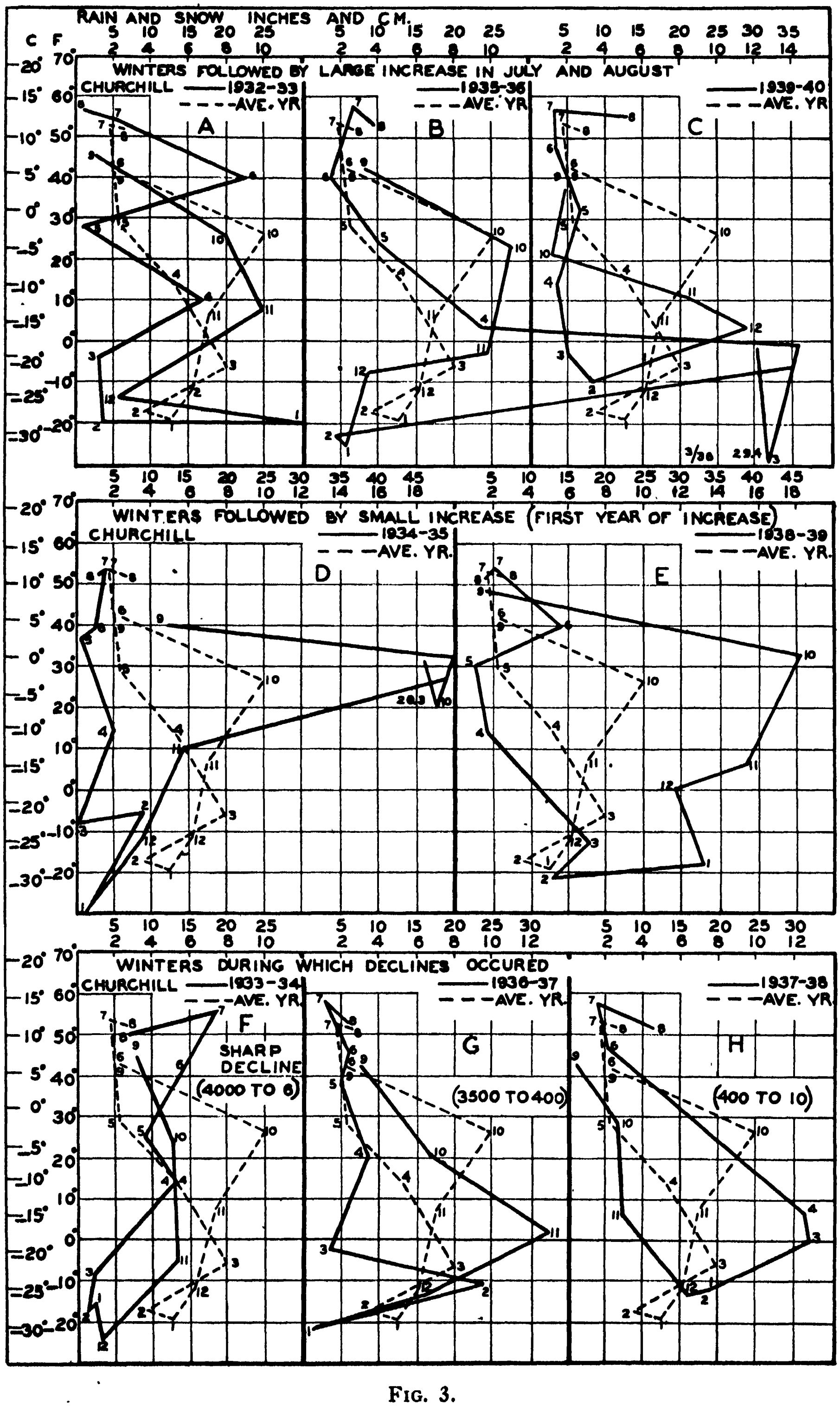

RAIN AND SNOW INCHES AND CM.
5 10 15 20 25
2 4 6 8 10
5 10 15 20 25 30 35
2 4 6 8 10 12 14
C F
-20° 70
-15° 60
-10° 50
-5° 40
-0° 30
-5° 20
-10° 10
-15° 0
-20° -10
-25° -20
-30°
WINTERS FOLLOWED BY LARGE INCREASE IN JULY AND AUGUST
CHURCHILL ——1932-33
- - - -AVE. YR
A
——1935-36
- - -AVE. YR
B
——1939-40
- - -AVE. YR
C
3/38
29.4
5 10 15 20 25 30 35 40 45
2 4 6 8 10 12 14 16 18
WINTERS FOLLOWED BY SMALL INCREASE (FIRST YEAR OF INCREASE)
CHURCHILL
——1934-35
- - -AVE. YR.
D
28.3
——1938-39
- - -AVE. YR.
E
5 10 15 20 25 30
2 4 6 8 10 12
WINTERS DURING WHICH DECLINES OCCURED
CHURCHILL ——1933-34
- - -AVE. YR.
F
SHARP DECLINE
(4000 TO 6)
——1936-37
- - -AVE. YR.
G
(3500 TO 400)
——1937-38
- - -AVE. YR
H
(400 TO 10)

Fig. 3.

in the following pages, but all should be carefully checked. There are various weather records wanting at critical points or quite probably it would be possible to speak with greater certainty, since there is considerable correlation between recorded weather conditions and the fluctuations in lemming abundance.

Climographs (fig. 3) in many cases bring out characteristics of a year's weather quite clearly and supplement the graphic outline in figure 2. There are three years of rapid increase and two years of decline which may profitably be shown by these climate diagrams.

Increases in Population (fig. 2).—There were maximum populations in 1929, 1933, 1936, 1940. The winter conditions preceding summers in which the population was built up were characterized by heavy snowfall and high winter temperatures at Churchill.

The 1929 Increase.—During the winter before the 1929 maximum there was heavy snowfall at Port Nelson (no Churchill records) and high winter temperatures at Churchill.

The 1933 Increase.—The population increase followed a snowfall of a little more than average amount, distributed from October to June, and a mild December and January. The temperatures of July and August were above normal. Trapping about July 20 showed 20 times as many lemming per 100 traps out for one night as in 1932. There was a definite but small population of about two lemmings per hectare in 1932, probably an increase of at least twenty to thirty fold from 1931. Unfortunately the 1931 (Oct. to Dec.) snowfall was not recorded but July to January temperatures averaged 5.6° F. above normal. December was 1.5° below normal and January 6.9° F. above normal, suggesting a favorable year. Trapping for 150 trap nights secured all the lemmings on two hectares (5 acres) in 1932. In 1933 the number rose to a little more than 40 caught per hectare per 100 trap nights on a similar two hectares. Furthermore, the lemmings on the 1933 area were evidently not all secured as all traps not catching lemmings were sprung. This large population in 1933 followed a dry autumn and the lemmings were on low ground as they were in 1932 when the rainfall of the preceding autumn was not recorded.

FIG. 3. Climographs showing the conditions during winters which were followed by sharp increases the next summer, and in which the population decreased sharply at Churchill. Normal year is shown in a broken line. The inches of rain and of snow were added together for the months in which both fell.

A–C. Showing the conditions in winters which were followed by summers in which there was a large reproduction leading to a high maximum in early autumn.

A. (1932–33.) The rise in population of 1933 followed this winter. Heavy snowfall, normal winter temperatures, and a warm July and August are noteworthy.

B. (1935–36.) There was a rise in population in the summer of 1936 following a cold midwinter with a very heavy fall of snow of 69 inches (10 hr. average, 48 in.) and October, November, and March favorable.

C. The 1939–40 increase followed an unusually mild winter, all months from November to April inclusive were from 4° to 13° F. above normal and snowfall was heavy beginning in November.

D–E. Showing years of small increase. There was probably an increase following the 1934–35 winter, unfavorable in the second half but favorable in the first half. Note heavy October snowfall.

E. There was probably an increase in the latter part of the summer of 1939 following the 1938–39 favorable winter.

F–H. Showing years characterized by winter declines.

F. The sharp decline in the winter of 1933–34 characterized by low temperatures and very little snow throughout. The decrease of from 4000 to 6 per 100 hectares (250 acres) is estimated from trapping.

G. Winter of moderate decline, a cold October and November low monthly minima (see fig. 2). Little snow in October; November considerable, but other months less than average. Decline estimated to be from 3500 to 400 individuals per 100 hectares.

H. A bad year; the first half being with very little snow, high winds September to November (see fig. 2); decline to a low minimum estimated to be from 400 to 6 individuals per 100 hectares (250 acres).

The 1936 Increase.—The winter of 1934–35 (fig. 3D) was favorable in the first half and unfavorable in the last half. The reports for the summer of 1935, however, showed a very small population in that year, but this was based on the report of a single naturalist; the number of observers was less than in other years.

The 1936 reproductive period began with a population in June and July which indicated that there had been an increase in the summer of 1935 over the extreme minimum of 1934. The population in June 1936 was probably the equivalent of that in 1932 but with the lemmings limited to sandy ground following a small excess of rain in September and 1.3 inches in October in addition to 9.4 inches of snow. The increase followed a winter with heavy snowfall especially in October, November and March and some sub-normal temperatures of small magnitude (fig. 3B). May and June were exceptionally cold and the young appeared late. Trappers reported them scarce during the late winter. Quite possibly a heavy cover of snow caused lemming to be seen less readily and trappers' reports were less accurate.

The 1940 Increase.—The winter of 1938–39 had the largest snowfall (75.0 inches) in the ten years of records at Churchill. The early summer of 1939 showed one of the lowest populations in the ten years of observation but in the preceding year the lemming population was similarly low. The late summer reproduction is not known as we found it necessary to leave the tundra, July 10, but some building up of numbers can be assumed as a basis of the favorable conditions. It is necessary to go back to the autumn of 1938 to understand the probable conditioning of the animals for the 1940 increase. The heaviest snowfall came in October (1938), 17.1 inches, November 15.2 inches, and December and January (1939) each approximately 12 inches. Only March and April snowfalls were below average. The October–January temperature averaged 5° above normal while the February–April averaged 5° below normal. Such conditions favor reproduction in the following summer and an increase in 1939 is an essential basis for the large population which followed in 1940. The winter of 1939–40 (fig. 3C) was very favorable as to both temperature and snowfall; there was a large increase and many lemming were reported for the September–August period of 1939–40. A second year of abundant lemmings followed the 1940–41 mild winter (fig. 2).

Decreases in Population.—Decreases may or may not take place suddenly. The 1933–34 decline was sudden and dramatic. An inspection of figure 3F shows that the deviations from average conditions in 1933–34 were extreme. The eight months of fall, winter, and spring were below normal in temperature. Further details are in the caption of the figure.

The 1936–37 decline was less sharp than that of 1933–34. It was accompanied by light snowfall and subnormal temperatures. There were two cold periods in November, one in the middle of the month and one at the end with − 22° to − 23°. Snow was scattered throughout the month, falling on 14 days in small amounts; on some days it would thaw. The wind velocity in November was high (fig. 2). From the middle of December to February 19 very little snow fell and practically the entire period was below normal in temperature (fig. 3). However, temperatures were higher, and there was a much greater snowfall than in 1933–34; the critical period included four months below normal in snowfall but only two months below normal in temperature. January, March, and April were especially low in snowfall. The decline was, however, relatively much smaller than in 1933–34 and was followed by a decline continued through 1937–38 and 1938–39 (Sept. to Aug.), a minimum population occurring in the early summer of 1939.

The 1940–41 decline appears to have been still smaller than that of 1936–37. However, only inadequate reports are available from our sources. Chitty and Nicholson, 1942, indicate a distinct decline in part of our area.

Spring Thaws and Other Factors.—A report from I. H. Smith covering the spring thaw of 1941 near Tanane on the shore of Hudson Bay states, "Mortality was high due to exceptionally deep snow which on melting drowned countless numbers." This is a natural result of the mild winter and the very heavy snowfall which preceded the thaw.

There appears to be little correlation between large numbers of lemming and sunspot numbers or ultra violet light, as observed at Mt. Wilson; the lemming maxima did not occur in the years of sunspot maxima (1928 and 1938–39) but just before and after as was the case with the chinch bugs (Shelford and Flint). No valid conclusions can be drawn from such a short period of observation.

Disease.—Elton ('42) appears to favor the idea that disease is the cause of rapid declines. The 1933 mouse population at Churchill was large, but there was a decline to a low minimum between August and June of the following year. Obviously many mice died. Since there were little snow and exceptionally low temperature in December, it was assumed that the animals froze to death in the winter of 1933–34. There were reports from numerous sources that many mice were found dead in burrows, runways, and nest balls as soon as the surface thawed in the spring of 1934. The skeletons found by the writer and several ornithologists in June and July were those of mice. Remains of dead mice were common elsewhere in July, 1934. Archdeacon Ferris reported similar conditions at York Factory. Indians had brought in some skeletons of mice and he himself had found others. This was regarded by the observers as unusual and was not reported in connection with any other population decline. It appeared that the severe conditions had killed off most of the mice but there is no proof that disease was not a factor.

No lemming remains were found in old runways in the spring of 1934 though this species had declined from a maximum to a low minimum during the same period as the mice. If lemmings had died of disease, *skeletal and other remains should have been found* in the following spring and summer. There is furthermore no evidence that lemmings died as a result of low temperatures. They are a strictly northern species and Churchill is near the southern limit of their range, while the great bulk of the Microtus population is *Microtus drummondi*, which ranges southward into the United States. The tundra mouse (*M. aphorodemus* Preb.) is not common at Churchill.

A small amount of snow probably makes lemmings easier prey for their enemies. The numerous lemming remains in the pellets of owls and the reports that other predatory birds were present, for the first time in several years, led to the conclusion that the lemming decline of 1933–34 was due to predation during the autumn and winter when the reproduction was slowed or had stopped. Furthermore, unusually low temperatures tend to increase the food demands of birds.

Chesterfield, Resolution Island and Nottingham Island.—Although additional species of rodents were present with the lemmings in these more northerly areas where reports of Chitty and Chitty on mixed populations are available, weather records were examined to see if the relations were similar to those found near Churchill. In making these comparisons the reader must keep in mind that the increase occurs mainly in June, July, and August, and the emphasis is on the trapping season, which falls principally in the period from September through May.

Chesterfield.—In the immediate vicinity of Chesterfield a decline in numbers of lemming, through the observation periods of three years, 1935–36, 1936–37, and 1937–38, is indicated by Chitty and Chitty ('41).

In the 1935–36 snowfall for November was only a trace on the second of the month and the monthly mean temperature was 11.7° F. below normal, a less favorable condition than at Churchill. This was possibly sufficient to interfere with reproduction and to cause the decrease reported.

In 1936–37 at Chesterfield temperatures were 3.4° to 14° below normal in the September through May period. October temperatures were lowest with a – 4° minimum at midmonth and a – 22° minimum on the 31st. But September through January snowfall was above average. In comparison with conditions at Churchill where there was a lemming increase (fig. 2); this winter probably only unfavorable enough at Chesterfield to interfere with the 1937 summer increase.

In 1937–38, a decrease was reported. On the other hand the 1937–38 winter was favorable as to snowfall and there should have been increased reproduction in the summer of 1938 which would show in the 1938–39 report. However, "No change" was indicated at Chesterfield, but an increase was indicated in the area to the south of Chesterfield. The favorable winter of 1938–39 followed giving two favorable ones in succession. These two preceded a large increase in the summer of 1939, which is recorded in the 1939–40 Chitty report. This increase came a year sooner than at Churchill. Since there is a second species of lemming and a different species of Microtus at Chesterfield, further investigation is needed.

Nottingham and Resolution Islands.—The weather conditions and the decline and increase of lemmings were analyzed for the weather stations in Hudson Straits. At Nottingham Island (400 miles east of Chesterfield) the reported increase in 1936–37 followed a year (1935–36) with all months above average temperature except November and May; snowfall above average in November and May. January (1936) snow was below average but temperature 2.9° F. above the monthly mean and both December and February had more than normal snowfall.

An increase was also reported for 1937–38. This followed the favorable winter of 1936–37 and the reproductive period, large population of that observation period. Snowfall was approximately normal and four of the eight winter months (1936–37) were from 1.6° F. to 8.3° F. above normal. The 1938–39 decrease could have resulted from a January and December which were both below average in snowfall in combination with low temperatures in February and March and almost complete absence of snowfall in these two months.

At Resolution Island 850 miles east of Chesterfield and 450 miles east of Nottingham Island.—The weather reports are too incomplete to use until 1936–37. The island climate is influenced by the Atlantic and is much milder than at Nottingham Island. In 1936–37 January to March were above normal in temperature and an increase in lemming was reported. The following year (1937–38) was again warm in midwinter and snowfall was unusually heavy. The thawing of 220 inches instead of the average of 90 inches at the end of the 1937–38 period could have been disastrous to the population but the remnants should be a vigorous breeding stock capable of increasing. The mild winter of 1938–39 was warm and the snowfall of the first half above normal. These conditions would favor the development of a large population the following summer which was recorded as the 1939–40 increase.

DISCUSSION

Correlations between weather conditions and the increases and decreases in the numbers of lemming have been pointed out. The manner in which weather operates on the individual animal is, however, not at all clear due to lack of knowledge of the life history, especially the length of the breeding period. It hardly seems probable that reproduction goes on during the cold months but the number of litters may well be increased by an additional one or more in the mild favorable years. There is evidence of a large number per litter in favorable years but this is based on limited observations during three seasons. Extreme winter cold without protecting snow can hardly fail to reduce reproductive capacity. The nature of the problem, however, calls for considering a large destruction of lemming by predatory birds and mammals. There is likewise abundant evidence of the increase in numbers of predatory birds probably by movement into the Churchill area when lemmings are abundant and their decrease or emigration when lemmings are few.

The studies of the Bureau of Animal Population (England) summarized by Chitty and Chitty ('41) for 1939 and 1940 shows that lemmings and mice are not at a maximum in all localities at the same time. This supports the idea of the migration of birds from place to place where small rodents are abundant. The observations elsewhere confirm the general findings at Churchill. An apparent population increase came one year earlier at Chesterfield than at Churchill and the cause is partially but not entirely evident from the weather data; some inaccuracies in data may have resulted from the presence of two species of lemming and the inclusion of mice with them. At Churchill the mice were investigated only from 1931–1936. The general conclusion from this is that the low points in numbers of lemming and *Microtus* coincide; however, mouse abundance precedes lemming abundance.

SUMMARY

The following relations between lemming population are indicated in a thirteen year period in six of which there were summer studies in the area concerned and reports from other naturalists in seven others. The indications have been stated in full because they require checking and elaboration over a much longer period.

At Churchill, Manitoba:

1. The local distribution of lemmings varies from year to year with some correlation with the autumn rainfall. Following wet autumns they were limited to the sandy ridges and generally distributed in drier years.

2. Weather at Churchill.—The propositions below are presented as tentative conclusions drawn from the weather analyses, examples of which have been presented.

a. The capacity of a lemming population to increase in a given manner is favored or determined by the following conditions (see fig. 3):

(1) Occurrence of average or more than average snowfall so distributed as to afford protection throughout the winter, in combination with temperatures above or near normal in the cold months (heavy snowfall with temperatures slightly below normal are not necessarily detrimental). The snowfall conditions in the first three months of winter are more important than in the later months.

(2) Temperatures above normal in July and August probably favor population increases.

b. Two favorable (or the first may be merely not unfavorable) years in succession are usually necessary to build up a peak population.

3. Choice of Location.—Summer rainfall, especially September and October rainfall, influences the choice of location in which over-wintering occurs—heavy rainfall, choice, well drained sandy ground: light rainfall, hummocks on low moist tundra. Wintering survival is

believed to be best on sandy ridges which facilitate burrowing.

4. Declines occur either suddenly or gradually due to conditions unfavorable to concurrent or later reproduction and to predation especially by wandering birds.
   - *a.* Very cold winters with little snow are accompanied by sharp declines of both mice and lemmings.
   - *b.* Less severe winters are characterized by moderate declines.

5. At Chesterfield and Hudson Straits, the published results of the Canadian Arctic Wild Life Enquiry are in accord with the findings near Churchill as regards weather relations.

6. Further definite progress in the field of cycles of abundance of lemmings calls for study of the life histories and individual habits throughout several years by a scientifically trained person on the ground.

ACKNOWLEDGMENTS

The writer is especially indebted to Dr. A. C. Twomey for extended reports for which he was not fully remunerated, to Mr. I. H. Smith (trapper), who sent reports on the condition of the lemming once or twice per year from 1932 to 1941, and Mr. Joseph Wright, naturalist and engineer, who reported on mice and lemmings in 1929–1930. A. H. Persien (trapper) confirmed Wright's findings as to lemming abundance and aided with later data. Thanks are due the following ornithologists who made important contributions: Mrs. Theodora M. Cope Fletcher, Dimmock, Pennsylvania; Mr. F. L. Farley, Camrose, Alberta; Mrs. A. Marguerite Heydweiler Baumgartner, Stillwater, Oklahoma.

The work was greatly enhanced by two Grants in Aid in Research from the National Research Council, one of $350.00 in 1932 and another of $130.00 in 1934. Also by a grant of $50.00 from the Graduate School Research Fund of the University of Illinois in 1936. These grants were essential to carrying out the work.

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THE LOCUST CONSOCIES IN THE DEVELOPMENTAL FOREST OF BULL RUN MOUNTAIN, VIRGINIA

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Introduction

The common locust, *Robinia pseudo-acacia* L., is more or less abundant in all the developmental deciduous forests in the Bull Run area, and elsewhere in Virginia. While it may infiltrate into an area after clear cutting of deciduous forest, it is not a frequent invader except where cutting has been followed by devastating fires. It may then become prominent as a secondary species, especially on the sandier, drier ridges.

Most of the former pastures on the lower slopes of Bull Run Mountain, once cultivated or pastured but long since abandoned, now have scattered or even dense stands of this secondary species. In some areas almost pure groves of locust cover many acres (figure 1). These woodlands are usually characterized by a very distinctive herb and shrub understory, and deserve particular mention in any study of early developmental stages of reforestation here.

The Locust Consocies

The locust, together with the sassafras, *Sassafras albidum* (Nutt.) Nees, the per-

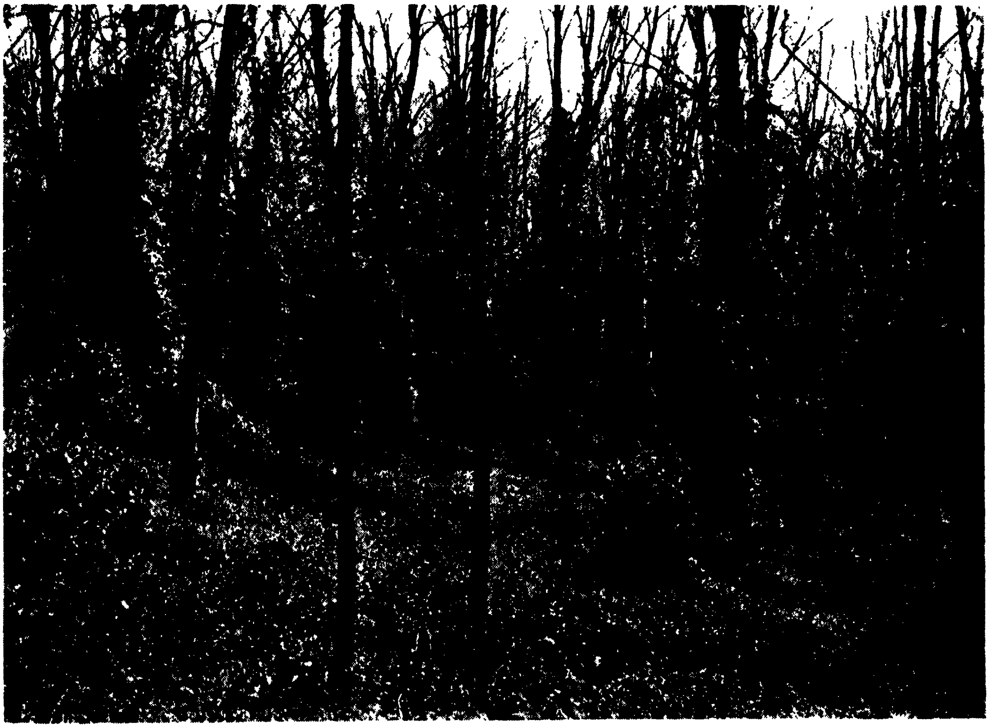

Fig. 1. Almost pure stand of locust, *Robinia pseudo-acacia*, on the west slope of Bull Run Mountain south of Hopewell Gap. This fine, dense stand appears to have developed upon abandoned cultivated ground about 25 years ago. Rampant climbing vines are Japanese honeysuckle, *Lonicera japonica*. In the foreground is a dense ground cover of pioneer species, *Stellaria media* and *Allium vineale*, with some pokeweed, *Phytolacca americana*. The shrubs are coralberry, *Symphoricarpos orbiculatus*. Photo. April 26, 1942 by H. A. Allard.

simmon, *Diospyros virginiana* L., the black gum, *Nyssa sylvatica* Marsh., and the flowering dogwood, *Cornus florida* L., are the most common broad-leaved pioneer trees in all old pastures of the Bull Run Mountain area.

Following the destruction of the chestnut by blight, the climax forest of this region is now mainly an oak-hickory assemblage in which the locust and sassafras are very minor components. The persimmon and the black gum are permanent components of this forest, the latter usually occupying a more conspicuous place on the better soils. The flowering dogwood is not only very prominent in the open associes of the pasture, but is a conspicuous element in the understory of the climax forest, owing to its tolerance of shade.

(*a*) *Relation of the Locust Consocies to Other Woodlands*

The presence of dense growths of scrub pine, *Pinus virginiana* Mill., of tulip poplar, *Liriodendron tulipifera* L., and of large areas of mixed hardwood forest of the climax type adjoining the locust communities affords excellent opportunities to make comparative studies of the various consocies.

The mixed hardwoods stand is a much older growth, representing an old cut-over forest, but the pine, tulip poplar and locust woods appear to be very nearly of the same age. The locust stands in contact with those of pine or tulip poplar have shown weak competitive ability. Wherever the pines and locusts have met, their communities in their present youthful condition have been independently maintained, since the deep shade of the former is entirely inimical to the light-requiring locusts as well as to their own reproduction. Conditions are unfavorable to the reproduction of the pines even beneath the better lighted locusts. The tulip poplars, on the other hand, becoming established on moister sites, have readily infiltrated into the stands of the locusts where they have not only grown rapidly, but are actually overtopping the latter. It is highly probable that the locusts, being legumes and active nitrogen-gatherers through the agency of nitrogen-fixing bacteria on their roots, are actually contributing to their own downfall by affording the tulip poplars larger supplies of the necessary element, nitrogen, than the latter would obtain in other associations.

The relation of the locusts to the heavy deciduous forests with a distinct climax facies, where the dominants are mainly oak and hickory, demonstrates plainly the purely temporary nature of the former as a developmental consocies. While barriers of shade and heavy ground detritus establish sharply confining limits around the locust groves, the oaks and hickories are gradually infiltrating into them, as in the case of the tulip poplars, probably also deriving considerable benefit from their contacts with this nitrogen-supplying type of forest.

A study of conditions within the dense locust woods gives definite evidence everywhere of its high requirement for light. Some detailed study was made of some of the better-developed consocies of the Bull Run Mountain area, where the most vigorous stands were about 25 years old as determined by ring count. A 10-meter quadrat was laid out in the midst of an exceptionally fine growth of straight, slender trees with the canopy about 35 to 40 feet above the ground, and the list of trees and shrubs was determined. In this area of 100 square meters forty trees were counted, thirty-three being locust, two ash, *Fraxinus americana* L., one tulip poplar, and four black cherry, *Prunus serotina* Ehrh. In addition to these there were five small trees of sassafras, one of black walnut, *Juglans nigra* L., about five feet high, one grape vine, *Vitis aestivalis* Michx., and one poison ivy, *Rhus radicans* L. The last two extended high toward the crowns of the locust trees.

Of the 33 locust trees, 12 (36.3 per cent) were dead, and 21 (63.6 per cent) were living. The dead trees were mostly small, the largest, a single tree, being only 3½ inches in diameter, and the smallest 1½ inches in diameter, all measurements being made at a height of one foot above the ground. The average diameter of the dead trees was 2.31 inches. The average diameter of the living trees was 4.64 inches, the largest of these being 7 inches, the smallest (one tree) 1½ inches in diameter.

It was obvious that the smaller locust trees were being eliminated from this stand, leaving an even-aged forest of very uniform height. There was no evidence whatsoever of reproduction anywhere beneath these trees, attesting the temporary nature of this distinctive successional forest on its site.

None of the young ash, tulip poplar or black cherry trees had died. These will probably persist and become components of the mixed hardwood climax forest which will ultimately displace these dense locust stands.

(*b*) *The Shrub Understory*

A very distinctive herbaceous and shrub flora thrives beneath the locusts. The most successful undershrub is the spice bush, *Lindera benzoin* (L.) Blume, which grows with exceptional vigor and in great abundance beneath the thin locust canopy (figure 2). In early spring the leafless branches of this shrub besprinkled with tiny yellow flowers contribute a veritable golden haze. Flowering dogwoods, redbud, *Cercis canadensis* L., and coralberry, *Symphoricarpos orbiculatus* Moench., are also more or less abundant elements of the shrub understory. The flowering dogwood and the redbud become permanent members of the understory of the climax hardwood

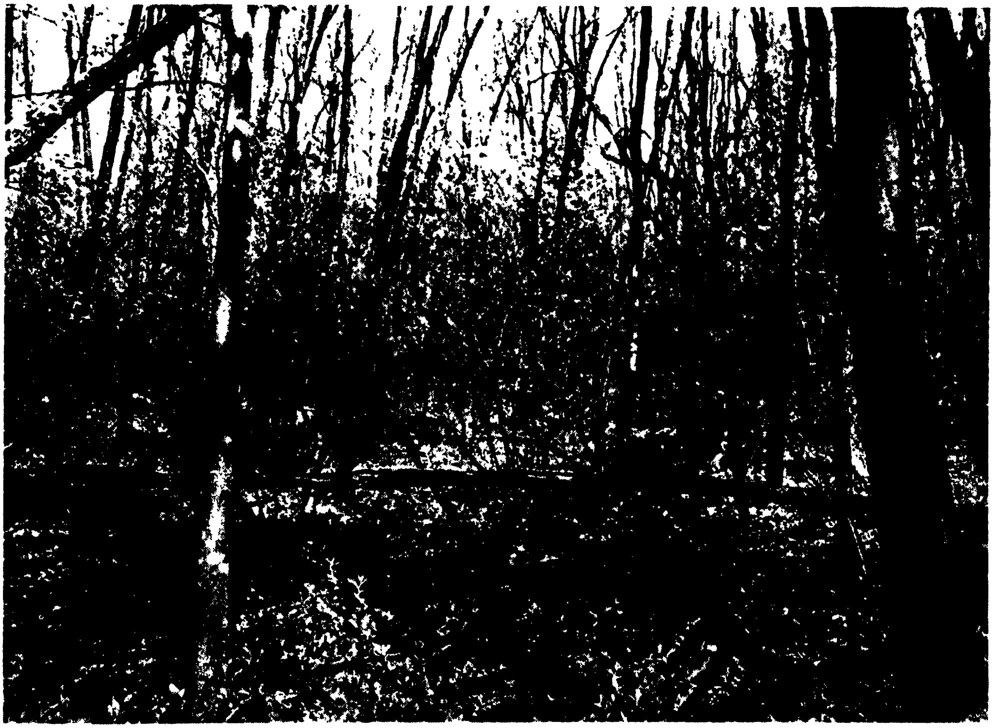

FIG. 2. View in another area of the locust stand shown in figure 1, where flowering dogwood, *Cornus florida*, and spice bush, *Lindera benzoin*, are abundant undershrubs. Photo. April 26, 1942 by H. A. Allard.

forests and also of the stands of tulip poplar. The spice bush does not establish itself in pine groves which occupy the drier sites and afford a dense shade. This shrub is less frequently found where tulip poplars are dominant and also grows less luxuriantly there. While it may appear as a minor constituent of the hardwood forests which have advanced well toward the climax type, it is usually confined to the moister soils and more open situations along streams. Two other shrubs, high blackberry, *Rubus frondosus* Bigel., and black raspberry, *R. occidentalis* L. occur in abundance and show exceptional vigor in some locust communities, the former in some situations developing almost impenetrable jungles of rank canes.

The coralberry is decidedly more successful in open situations, and appears to have been caught by the sudden invasion of the locust community into an old field or pasture. It appears to survive beneath these trees with some difficulty, for it develops a somewhat scraggy and etiolated growth-form. It would appear that here it has very nearly approached its minimum light requirements. It does not persist in the tulip poplar consocies which have also invaded old pastures, and is non-existent in the oak-hickory forests covering the Bull Run slopes. This shrub is a common constituent of many open pastures where it enters into strong competition with the grass, *Andropogon scoparius* Michx. Ultimately it gives way to such vigorous native pasture shrubs as sumac, *Rhus glabra* L., and the weedy trees of the secondary forest which include flowering dogwood, sassafras, persimmon, and a few other species.

Japanese honeysuckle, *Lonicera japonica* Thunb., becoming especially rampant and high-climbing in the well-lighted locust woods, often covers large areas with its heavy, strangling growth, and practically eliminates all native herbs. This introduced woody vine, even in the open pasture, cannot well compete with the heavy closed communities of broomsedge, *Andropogon scoparius*. Here its colonies remain small and circumscribed and are characterized by a more bushy and depauperate habit of growth than it displays in the locust woods. This vine makes little headway in the drier areas dominated by consocies of scrub pine and is almost or even entirely excluded from the climax hardwood forests of oak and hickory. It attains its greatest success on exposed banks and in the better lighted locust groves, where a thin layer of leaf litter is the rule, and where it finds greater quantities of available nitrogen, the probable contribution of the locusts. The striking contrasts of growth behavior shown by the Japanese honeysuckle in the open broomsedge pastures and in the locust groves may also depend upon differences in amounts of moisture as well as of nitrogen.

In the understory of the 10-meter list quadrat previously mentioned grew one small dogwood, eight small, ragged clumps of coralberry, four to five feet high, and twelve vigorous, much-branched clumps of spicebush, ten to twelve feet high. High blackberry, *Rubus frondosus*, was absent in this quadrat, but several plants of black raspberry, *R. occidentalis*, were present.

(*c*) *The Herb Stratum*

The herb stratum of the locust stands is especially striking and in some respects seems almost out of place in the woodland habitat. Here a number of native species of the climax forest meet a weedy flora peculiar to waste ground. The plants of both habitats grow here with exceptional luxuriance, the latter more especially showing a vigor comparable to that found in the nitrogen-enriched soils occurring around old house sites and barn yards.

The native wild plants of the locust groves, appearing in great abundance in some situations, are Jack-in-the-pulpit, *Arisaema atrorubens* (Ait.) Blume, rattlesnake fern, *Botrychium virginianum* (L.) Sw., and touch-me-not, *Impatiens biflora* Walt. Among the waste ground herbaceous plants the most common species are chickweed, *Stellaria media* (L.) Cyrill., bedstraw, *Galium aparine* L., pokeweed, *Phytolacca americana* L., gill-over-the-ground, *Glechoma hederacea* L., catnip, *Nepeta cataria* L., garlic mustard, *Alliaria officinalis* Andrz., wild garlic, *Allium vineale* L., bitter cress, *Barbarea vulgaris* R. Br., and bouncing-bet, *Saponaria officinalis* L. The grass, bottle-brush, *Hystrix patula* Moench, a typical species of the climax forest is also a vigorous component of the locust groves.

In vigor of growth and abundance garlic, *Allium vineale*, chickweed, *Stellaria media*, *Glechoma hederacea* and pokeweed, *Phytolacca americana*, were outstanding species beneath the locust canopy (figure 1). Of the three, chickweed is one of the least adaptable species. Some tufts of garlic, multiplying only from the basal bulbs, may occur in the tulip poplar consocies, and depauperate specimens may be found even in the broomsedge cover of the pastures. The chickweed, on the other hand, requires more or less exposed soil, especially during the cooler months of the year as its growth period extends from November to April. It cannot cope with the deep leaf litter of heavy deciduous woods of the climax type, whereas the smaller, thinner, less abundant and more readily decomposable leaflets of the locusts are not particularly detrimental to it. *Glechoma hederacea* shows a very similar behavior, and never occurs in the heavy deciduous mixed hardwood forests nor in the old well-developed broomsedge associes.

Phytolacca americana occurs in great profusion and attains giant stature beneath the locusts. These plants do not occur in the dense broomsedge pastures, nor in the consocies of scrub pines. They are not of general occurrence in the consocies of tulip poplars, and are entirely lacking in the heavy oak-hickory stands of the climax forest, except where openings occur, or where trees have been uprooted, exposing the naked soil.

In the particular quadrat studied pokeweed, *Phytolacca americana* L., very common in other locust communities, was entirely absent. Other herbaceous species were present, however, including field garlic, *Allium vineale* L., in such abundance as to contribute a tinge of uniform greeness to the area. Considerable jewelweed, *Impatiens biflora* Walt., was present, and one plant of anemone, *Anemone virginiana* L., was observed, the latter being a frequent forb of the well-established broomsedge cover in old pastures.

Discussion and Conclusions

The locust consocies affords a striking example of a temporary developmental type of woodland representing the earliest stages of forest succession in the Bull Run area. Its sparse foliage canopy, affording good illumination to herbs beneath its crowns, and the thin, small, readily decomposable leaflets which are never abundant enough to blanket the ground with a deep leaf litter furnish a type of habitat which is highly favorable to a number of shrubs and herbs in the understory. These never enter the more permanent pine or hardwood forests. A few of these herbs are native species, but the majority are introduced weed species which thrive only in open waste ground and especially in nitrogen-enriched soils around outbuildings.

It is obvious that the soil and habitat conditions on the forest floor in the locust consocies are far more favorable to all these species of the understory than is the dense, matted, broomsedge cover so highly developed in some old pastures of the Bull Run Mountain area.

In many respects the habitat conditions characterizing the locust consocies represent a striking transition stage between the old field and waste ground situation on the one hand and the typical hardwood forest environment of climax facies on the other. Some of the most typical native herbaceous components of the hardwood forest have entered the locust consocies, namely Jack-in-the-pulpit, and *Botrychium virginianum*. These plants never invade the old-field broomsedge cover or colonize the open fields and waste-ground areas around outbuildings, yet in the environment of the locust stands these native wildings may consort with a waste ground assemblage largely of old world origin.

One may ask why the stands of locust favor the distinctive herbaceous communities which are found beneath them while woodlands consisting of tulip poplar, pine or mixed hardwoods appear unfavorable to their growth. Although at present the actual causal relationships are quite unknown, there is reason to believe that conditions of some complexity obtain, involving not alone microclimatic influences, but changes induced in the physical, chemical and moisture relations of the soils.

While the writer has not been in position to substantiate the view with definite experimental evidence, it is indicated that generous supplies of nitrogen are contributed to the soil by the shallow-rooted locusts since these trees are legumes,[1] and the roots of these plants generally harbor nitrogen-fixing bacteria. This is attested by the exceptional vigor and stature of most of the plants growing beneath these trees.

There is reason to believe, also, that the shade conditions and leaf litter of the locust consocies almost or even completely exclude most of the competing old field grasses, more especially the broomsedge, *Andropogon scoparius*, purple top, *Triodia flava* (L.) Smyth, and Indian grass, *Sorghastrum nutans* (L.) Nash. The grass *Hystrix patula*, a woodland species, finds a suitable habitat here. This restriction imposed upon the development of the old-field grasses naturally reduces competition greatly and may be a factor in encouraging the ecesis of such weeds as *Stellaria media* and others of the open waste-ground class. It is possible that other factors may be involved in addition to chemical factors associated with an enriched soil, although the writer can bring no actual proof at the present time that such is the case.

The associations of plants in a given community are now known to be very complex. In some instances a definite herbaceous annual flora associates itself specifically with certain trees and shrubs. This has been shown by Went ('42) in a sociological study of plants in the Colorado and Mojave deserts in Southern California. He has found that certain annuals rather regularly associate themselves with certain desert shrubs, not only while these are living, but after they have died, so that such physical influences of the living shrub, as shading or other conditions, cannot operate. These preferential behaviors tending to bring certain plants into close relation with each other are supposedly due to highly specific organic chemical materials formed and liberated by the shrubs.

It is now known that in the rotations of various farm crops, all plants are not mutually beneficial in these artificially arranged successions. It is probably true that similar relations may hold in some instances in natural successions that are trending toward a climax vegetation. Went mentioned the very detrimental effect of the common grass *Imperata*, on plantations of rubber trees (*Hevea*) in Java, stating that "not only the production but even the life of plantation trees such as *Hevea* ('42, p. 113) may be endangered by this grass."

Kooper ('27), who has studied the weeds appearing after the plowing of the rice fields in the plains of Pasuruan in East Java, claimed that the distinctiveness of a particular weed flora begins from failures of germination of certain species, and that there is a mutual influence of the plants upon each other. Went found similar conditions to obtain in the weed relationships near Semarang in middle Java.

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[1] There is some evidence that the honey locust, *Gleditsia triacanthos* L., may not be a nitrogen-fixing plant.

Until very careful experimental studies have been made no such definite conclusion can be drawn with respect to the specific weed communities found in the locust stands of the Bull Run Mountain area. It may well be, however, that these plants find a highly beneficial habitat related not only to the nutritional nitrogen but to other specific organic substances especially favorable to ecesis of a particular flora.

It is interesting to note that the locust, generally, is regarded as beneficial to other plants adjacent to or associated with stands of these trees. Ferguson ('22) in Pennsylvania found that a marked increase in average height and in average d. b. h. was shown by catalpa trees planted at decreasing distances from the locust grove. This was apparently associated with the increased nitrogen supply contributed by the locusts with their root nodules. Miller and Tehon ('29, p. 234) stated that it is claimed "that barren sand planted to Black Locust will become fit, in five years, to support bluegrass." McIntyre and Jeffries ('32) noted that most trees are benefitted by planting with locust due to the increase in total nitrogen of the soil.

Chapman ('35) studied in some detail the effects of locust plantings upon other trees, using experimental plots of various trees. Among these were catalpa, white ash, tulip poplar, black oak and chestnut oak. He found a consistent and very marked decrease in average height and average diameter, as the distance of the rows of these trees parallel to the rows of the locust trees was increased. There was also a very marked decrease in total nitrogen of the soil, which was examined to a depth of 6 inches. When the amounts of nitrogen were computed for an acre six-inch depth on the basis of 2,000,000 pounds of soil, there was a range of 3900 pounds of nitrogen for the nearest plot, falling to 1800 pounds for the plot farthest removed from the locusts, this being 72 feet away. When the nitrogen relations of small plots of locust and of Chinese elm, *Ulmus pumila* L., were compared, an appreciable decrease in total nitrogen was found for the second year in the elm plots. On the other hand, the soil of the elm-locust plots showed a significant increase in total nitrogen in the same period.

Gorman and Merkle ('38) made a study of the soils in locust groves as influenced by locust litter. They found that the soils appeared to be increased from a pH of 5.00–5.5 nearly to the neutral point 7.00, by the decay of the locust litter. They concluded that the basic nutrients calcium, potassium, and magnesium were withdrawn from below and deposited upon the surface by decay of the leaf refuse.

It is obvious that the quick-growing and short-lived locust, owing to its intolerance for shade, and the requirements of its seedlings for naked soils, is not qualified to assume the role of a potential climax tree. Its distribution generally indicates a tree of xeric constitution, since it occurs most frequently in dry habitats, such as sterile, rocky, cut-over slopes, on burns, and in the poor soils of dry pastures. Its xeric tendencies are shown by its abundance on the steep, dry, sparsely vegetated shale barrens of the Massanutten and other mountain areas in Virginia, although there characterized by depauperate growth. It is not physiologically constituted to compete with the hardwood forest in more mesic situations.

The tree is attacked by a number of destructive insect pests including the locust borer, *Cyllene robiniae* Forst., and the locust leaf miner, *Chalepus dorsalis* Thunb., both of which make existence difficult for it even under the most favorable conditions. The larval stage of the latter insect, a flea beetle, may also completely destroy the chlorenchyma of the leaves each season, so that they appear brown and lifeless as if scorched with fire, more especially in dry seasons. In spite of this repeated seasonal injury the trees survive. Since they grow generally in dry, sterile soils they must be subjected to a further reduction in their normal water absorption as a result of the leaf destruction. This resistance to such reduction in water absorption during the hottest weather of midsummer further attests the strongly xeric nature of these trees, and their high adaptability to such trying conditions.

SUMMARY

The locust, *Robinia pseudo-acacia* L., is a frequent constituent in the early stages of the successional forest of Bull Run Mountain, Virginia. It also occurs on burns on the more barren ridges.

In some areas it has developed almost pure stands, with straight, tall trunks carrying the foliage canopy about 35 to 40 feet above the ground. These stands are characterized by a herb stratum, comprised of many weeds of open waste ground, including such plants as *Allium vineale* L., *Stellaria media* (L.) Cyrill., *Phytolacca americana* L., together with some native members derived from the climax forest. These weeds grow in abundance and thrive with notable vigor in the locust stands. They are almost or entirely absent in the consocies of scrub pine, tulip poplar, and in the mixed hardwood forest tending toward the climax type.

Good conditions of illumination, a thin and readily decomposable leaf litter, and added supplies of nitrogen formed by nitrogen-fixing bacteria associated with the roots may be responsible in part for the distinctive weed associations developing beneath the locusts. While there is no positive evidence at hand at the present time, it is possible, also, that specific organic substances highly favorable to these particular weeds may be contributed to the soils beneath the locusts, and encourage a selective assortment of weeds.

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TOLERANCE OF THE SNAIL *THAIS FLORIDANA* TO WATERS OF LOW SALINITY AND THE EFFECT OF SIZE

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Introduction

The snail *Thais floridana* is one of the prominent molluscs of the Gulf coast. It is well known to oyster fishermen there as a predator of oysters. The size of this animal is considerably smaller in the vicinity of Pensacola than it is west of the Mississippi; also, the architecture of the shells is typically different. *Thais floridana floridana* Conrad from Santa Rosa Sound is a smooth-shelled form, whereas *Thais floridana haysae* Clench, obtained in Grand Bayou and from Sugar House Reef, Barataria Bay, La., is characterized by a double row of protruding knobs about the largest whorl of the shell. The identification of these two geographical varieties was kindly made by Dr. Paul Bartsch of the United States National Museum, from specimens sent to him. Snails from various localities were used together in these experiments in order to obtain a complete range in size. There did not seem to be any specific difference in their reaction to the experimental conditions.

In view of the fact that salinity is one of the important ecological variables of confined coastal waters, such as obtain in Santa Rosa Sound and Barataria Bay, a study was undertaken of the effects of salinity changes, particularly from high to low salinity, on the snail Thais. The significance of the study is twofold. First, there is the consideration that animals living in or near the tidal zone must in one way or another exhibit a high degree of tolerance to salinity changes in order to survive. A study of behavior in relation to this environmental factor is therefore of general importance to the great animal majority which makes the littoral zone the most populated region of the sea. Secondly, inasmuch as the snail under investigation is an important enemy of oysters, and in view of the fact that grounds where both the oyster and the snail live are normally subject to dilution with river water, a study of the salinity tolerances of Thais may have practical value in determining the location of planted oyster beds. This hypothesis is based, of course, on the supposition that the oyster itself possesses a higher range of tolerance than does the snail. All information now available (communication from Dr. A. E. Hopkins) indicates that such is actually the case.

The work here reported was done at the U. S. Fish and Wildlife Service Laboratory at Pensacola, Florida, during the first half of the year 1942. For the use of the laboratory and for extending opportunities for studies in the field, I am deeply indebted to the Director, Dr. A. E. Hopkins. Material was collected locally; and from Barataria Bay by courtesy of Mr. J. N. McConnell of the Louisiana Department of Conservation, who kindly allowed the use of the facilities of the patrol boat "Louisiana" for the purpose.

Experimental Methods

Snails freshly collected at intervals of about two weeks were placed in a laboratory aquarium of running sea water and permitted to acclimate themselves for at least 24 hours. Only those were used in the experiments which gave evidence of a high degree of vitality by righting themselves and climbing up the sides of the aquarium. Solutions of different salinities were made up by diluting sea water with tap water from the regular drinking supply, which was filtered rain water. Three liters of solution, to a depth of 7 cm., were placed in each of the necessary number of cylindrical dishes, 10 inches in diameter. The salinities were 0, 3½, 7, 10, and 14 p.p. 1000 by dilution; and from about 17 to 28 directly, as the sea water varied from time to time. In some of the experiments, when the salinity of the running sea water dropped excessively low, stored aged sea water of high salinity was utilized to make the dilutions. Washed air was continuously pumped in a fine stream into each dish. All dishes were placed on a laboratory table where the sunlight was not allowed to play upon them. There was no method of temperature control available. The temperature of the solutions ranged from a low of approximately 12° in February to a high of about 28° in June, but the variation during a single experiment was never more than 8 degrees and often only 2 degrees. All solutions of an experiment were at any one time within ½ degree or less of each other; so that, the effect of temperature on the comparative results in different salinities may be completely ruled out.

The pH of the solutions varied within narrow limits. The entire range was from approximately 8.0 in sea water to about 7.4 in tap water. In the course of 48 hours, at which intervals the solutions were usually changed, the pH rose 0.1 or 0.2 in salinities of 0 to 10 p.p. 1000. The greater alkalinity may be due to lime released from the shells. In salinities of 14 and above, the pH dropped as much as 0.3; the acidity possibly being due to greater activity of the animals at higher salinities.

In almost all of the experiments 10 snails were placed in each dish; 4 were small and ranged from 1.2 to 3.0 cm. in length, averaging about 2.4 cm.; 3 were medium sized and averaged from 3.5 to 5.0 cm. in length; 3 were large and averaged from 7.0 to 8.4 cm. The volume of all the snails in one dish was, including shells, never more than approximately 200 cc. as compared with 3000 cc. of solution.

The animals were placed on their backs in the experimental dishes and overturned again, if necessary, every 24 hours. The numbers which righted themselves were noted each day and those unable to right themselves were termed "immobilized." Also, records of sensitivity to mechanical stimulation were kept for the duration of the experiments. At the close of an experiment, the specimens were returned to undiluted sea water for observations on recovery. After a period of up to 3 or 4 days, those which showed no sensitivity to mechanical stimulation were recorded as dead. Almost always these had a detectable odor of putrefaction.

Eleven separate experiments of the kind described were carried out, involving a total of over 600 animals.

Experimental Results

General Observations.—When snails were transferred from the laboratory aquarium into the experimental solutions, they began to right themselves within 10 minutes if there was little or no change in salinity. If placed in tap water they closed up tightly and the operculum remained closed until death occurred. In a salinity of 3½ p.p. 1000 they at first closed, but after 24 hours or more, showed a small aperture of perhaps 10°. Siphons were fully contracted. In 7 p.p. 1000 the operculum opened 30° or more and the siphons were protruded into the siphonal canals. At this salinity mechanical stimulation, during the first stages of the experiment, caused quick withdrawal. In later days a few snails were able to right themselves. In 10 p.p. 1000 snails opened 90° or more the first day. Siphons extended beyond the canals. Some righted themselves during the first 24 hours. In 14 p.p. 1000 and above, almost all righted themselves within 24 hours.

At the salinities in which the snails were able to right themselves, there was a progressive increase in holdfast power easily detectable when the animals were pulled loose. There was also greater mobility and greater tendency to climb with increasing salinity. As concomitant evidence of greater activity there was a progressively greater amount of feces discharged. In the lower salinities of these experiments it was generally observed that a swelling of the foot occurred during the first few days, followed later by a secondary shrinkage.

Shock.—In transfer from a natural salinity of approximately 14 p.p. 1000, or somewhat above, in the aquarium to the same salinity in the experimental dish, the righting reaction, i.e., simply overturning, was well under way within ten minutes as already noted. In going to salinities of below 14 there was evidence of injury. Salinities above 14 were increasingly more favorable for the activity and and life of the organisms. It is of interest to note, therefore, that the righting reaction took place more quickly when there was no change at all than when the snails were transferred to a higher salinity. Similarly, when transferred from 14 p.p. 1000 to a lower level the righting reaction, if any, took longer than when there was no change in salt concentration. This first effect of change in salinity is termed "shock." Figure 1, in the curve for the righting reaction when snails were transferred from 14 to 28 p.p. 1000, best illustrates this phenomenon.

In all of the experiments the factor of shock was introduced twice; first when the snails were placed in the experimental solutions, and secondly when they were returned to sea water for survival tests. It is of interest to note that there was no clear evidence that the second shock added appreciably to the injury sustained in the solutions of low salinity.

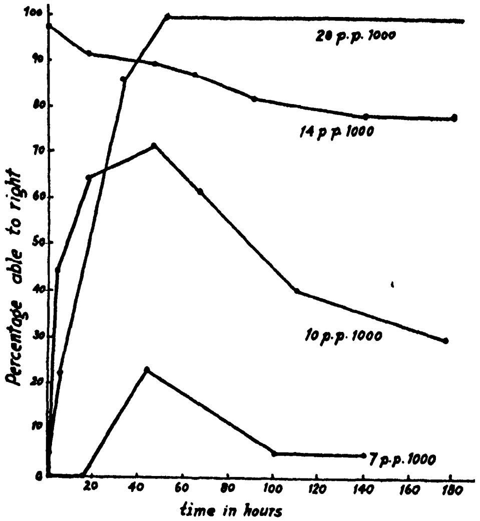

FIG. 1. Ability to right in various salinities, after acclimatization in 14 p.p. 1000. (In 0 p.p. 1000 and in 3½ none can right themselves.)

Immobilization.—Occasionally in salinities of 14 (to a slight extent), and increasingly in lower salinities, recovery from shock, as evidenced by the ability of the animals to right themselves, was not complete. This is shown in figure 1. In 0 and 3½ p.p. 1000 all were immobilized. In 7, 10 and 28 p.p. 1000 a peak of recovery was reached in 40 to 50 hours after introduction into the respective solutions. The peak is interpreted as a measure of the interaction of the process of recovery from shock, with the onset of injury. Falling off after the peak is interpreted purely as injury due to low salinity. According to these definitions it is to be noted that in 0, 3½ and 7 p.p. 1000 there is little or no recovery from shock. Injury is also marked in 10 p.p. 1000. In 14 p.p. 1000 there is a gradual onset of a relatively small amount of injury. In 28 p.p. 1000 there is full recovery from shock and no subsequent injury. The graph at each salinity is based on results with about 100 snails. The phenomenon of immobilization is clearly summarized in figure 2. Each point represents the data from 109 snails, except at 14 and 17 p.p. 1000 respectively, where 100 and 79 snails were involved.

Injury and Death.—Immobilization in time is followed by injury and eventually

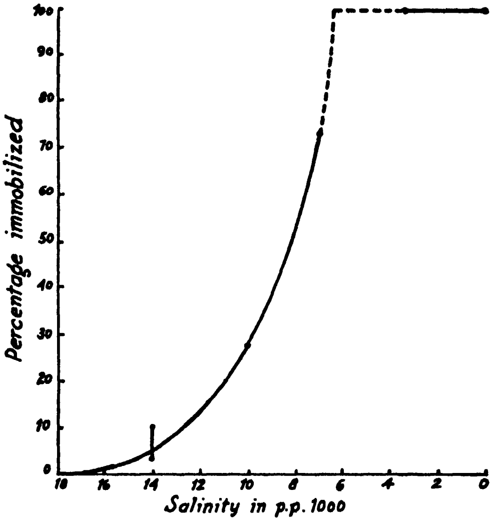

FIG. 2. Immobilization in waters of low salinity.

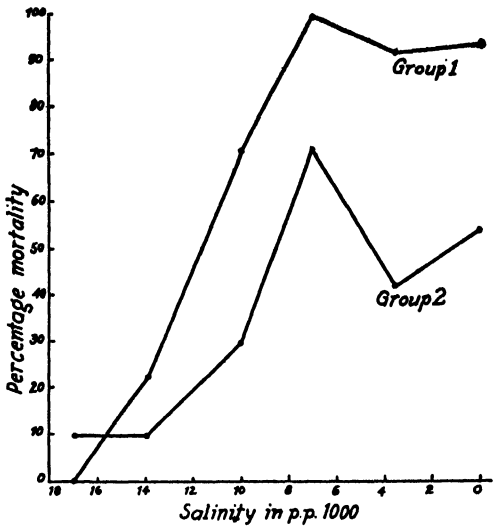

FIG. 3. Mortality in waters of low salinity.

by death. The lethal effect was determined by replacing all the snails in sea water of high salinity after sensitivity to mechanical stimulation had been lost, or almost lost, by those exposed to the lower salinities (0, 3½, 7). The results are given in table I. For summation, the experiments are divided into two groups. Those in which there was little or no difference between the effects of salinities 0, 3½ and 7, have been combined into Group 1. It will be noted that these are experiments of long duration (1, 2, 3 and 4) or of higher temperature (9 and 10). In Group 2 are the experiments where a differential effect was obtained in the lower salinities (Experiments 5, 6, 7, 8 and 11). These are experiments of comparatively short duration. Survival of Group 1 as compared with Group 2 is plotted in figure 3. By examining the curve of Group 2 an exceedingly interesting and unexpected result becomes apparent, i.e., the experi-

TABLE I. *Mortality in solutions of given salinity*

Salinity in p.p. 1000			0		3½		7		10		14		17–28	
Exp. no.	Exposure time in hours	Temperature in °C.	Dead	Total	Dead	Total	Dead	Total	Dead	Total	Dead	Total	Dead	Total
1	380	13–19	9	9	9	9	9	9	3	9	2	9	0	9
2	313	12–19	12	12	12	12	12	12	12	12	4	12	0	12
3, 4	188	18–23	17	18	16	18	18	18	11	18	3*	9	0	18
5, 6	140	22–24	13	20	9	20	14	20	2*	20	3*	20	3*	10
7, 8	139	18–25	12	20	9	20	16	20	9	20	2	20	0	10
9, 10	113	25–28	20	20	20	20	20	20	16	20	2	20	1	10
11	74	26–27	2	10	3	10	6	10	4	10	0	10	0	10
Group 1. Exp. 1, 2, 3, 4, 9 and 10 % mortality			98		97		100		86		16		2	
Group 2. Exp. 5, 6, 7, 8 and 11 % mortality			54		42		72		30		4		0	

* Smothered and eaten by larger snails.

mental procedure at 7 p.p. 1000 has a significantly more lethal influence than at either 0 or 3½ p.p. 1000. Above 7 p.p. 1000 there is the to be expected falling off of mortality. At 14 p.p. 1000 mortality is slight, and was due for the most part to the fact that the small, partially or completely immobilized snails were captured and eaten by the larger ones. At 17 and above, there is practically no mortality.

Rate of Recovery.—In experiments of short duration there was an appreciable amount of recovery even after exposure to very low salinities, as shown above, when the snails were replaced in sea water. Maximum recovery always equalled or exceeded the expectation obtained by examining the snails in the experimental solutions immediately before the recovery test, i.e., a snail which had not completely lost sensitivity to mechanical stimulation usually recovered after transfer to sea water of high salinity. Maximum recovery has been used as a measure of mortality in this paper. A brief consideration of the rate of recovery has certain additional interest. The data are derived from seven experiments in which the average exposure time was 146 hours at an average temperature of 22°. The recovery time given in table II is approximate since after the first few hours, during which the snails were observed closely, 8 or 10 hour intervals may have elapsed between examinations. Nevertheless, times of recovery as given in the table present a reasonably accurate picture of the rate. It is apparent that rate of recovery from exposures to salinities which soon result in death, varies inversely with the salinity, i.e., from 0 to 10 p.p. 1000, the fastest recovery is in the lowest salinity. This may be due to the fact that in the lower salinities the operculum is kept more tightly closed, and the extent of osmotic injury is, in all probability, less. In snails from 14 to 28 p.p. 1000, recovery time is taken to represent recovery from osmotic shock.

TABLE II. *Recovery in 24 p.p. 1000 after exposure to given salinities*

Salinity	0	3½	7	10	14	28
Number of snails	68	68	68	68	59	48
Number recovered	22	28	10	42	51	48
Time in hours	27	33	36	39	23	2½

Effect of Size.—Throughout these studies it was noticed that small snails behaved somewhat differently from large. In the solutions where recovery occurred at all, the small ones were the first to recover from the shock of transfer. But they were also the first to succumb to the injury which followed shock, and eventual mortality was inversely proportional to size. The snails were measured in length with micrometer calipers, from the tip of the spire to the termination of the siphonal canal. Relation of length to volume was obtained by immersing 10 snails of each size in a graduated cylinder. The first five points in figure 4 are of local snails from Santa Rosa Sound. The last two points (7 and 7.7 cm.) are of Barataria Bay snails. It is of some interest to note that all points seem to fall on a single curve.

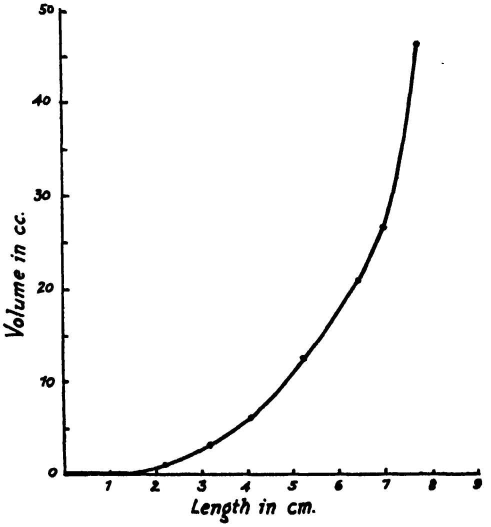

FIG. 4. Relation between snail length and volume.

The data which bring out the effect of size are derived from seven separate

TABLE III. *Relation of size to survival*

Snail length in cm.	2.4		4.8		7.5	
Salinity	Dead	Total	Dead	Total	Dead	Total
0	24	27	13	21	8	21
3½	26	30	13	24	7	24
7	29	29	19	24	15	24
10	29	38	10	29	8	30
14	10	24	2	18	0	18
Totals	118	148	57	116	38	117
Percentage	80		49		32	

experiments and are summarized in table III. For example, at salinity zero 24 snails of length 2.4 cm. were dead at the termination of the experiment and only three of the same size were alive.

PRACTICAL CONSIDERATIONS

From a practical point of view looking toward the control of the depredations of Thais, the phenomena of immobilization and death must be considered together. At 0 and 3½ p.p. 1000 the snails are immobilized and remain closed. At 7 p.p. 1000 they lie more or less open and insensitive. With respect to survival a minimal value is reached at 7. Below 7, and above, the percentage which survives increases. Not only is the direct lethal effect of low salinity most pronounced at about 7 p.p. 1000 but also at this salinity, lying open and immobilized, the snails would be most subject to attack by natural enemies. At 10 and above both percentage of immobilization and lethal effect decrease. From the practical viewpoint of control, therefore, a salinity of approximately 7 is optimal. Projects to control the depradations of the snail by "letting the river in" which have been suggested for the Barataria Bay area, for example, must therefore be carried out under close regulation, if at all.

Also, before experimental results can be applied, a careful study of field conditions is indicated. Fresh waters have a marked tendency to float upon waters of higher salinity, as has been observed frequently in the field. In the vicinity of Pascagoula, for example, when the surface waters were quite fresh, dredged oysters had their full salty flavor. Depth of oyster bottoms and turbulence of the surface would therefore be important considerations in determining whether introduced floating fresh water could penetrate to an effective level.

Lastly, it may be noted that the salinity of confined coastal waters, as at Pensacola, often drops extremely low. During the summer months of both 1939 and 1940 it went to the level of 4 p.p. 1000. Presumably more snails survived under these conditions than if the salinity had not dropped quite so low.

DISCUSSION

Few previous investigations appear to have been made on the survival of snails in waters of low salinity. Federighi (1931) reported that at temperatures of 24–26° C. death of *Urosalpinx cinerea* occurred in 10 days at salinities of 12 and 16 p.p. 1000, depending on the salinity of the water from which the snails were obtained. Stauber (address to the National Convention of Shell-fisheries Association, '41) exposed the same animal for 14 days at 20° C. and found that some could survive a salinity as low as 7 p.p. 1000. Neither of these two investigators appears to have varied the duration of exposure. This may account for the fact that they mention no break in the curve of survival with decreasing salinity; nor of any correlation with the size of the animals. These findings, with Thais, the present writer regards as of considerable significance, both theoretically and from a practical point of view.

With regard to the modifying influence of size, there are at least two observations by other workers which indicate that the phenomenon may be widespread. Scordia ('27) showed that young specimens of the Mediterranean mollusc, *Haminea hydatis*, can tolerate higher salt concentration than can old ones. Andrews ('40) observed that salinity, increasing in a natural salt pond over a period of years, led to a decrease in size of the snail, *Neritina virginea.* It may also be of significance (Hayes, '29) that the development of young snails is retarded in hypotonic media.

An interesting paper by Blum ('22) on *Teredo navalis* parallels the present work on Thais in some respects. With this animal, as with Thais, activity, by the criterion of siphon extension, falls off rapidly below 7 p.p. 1000. However, there was no break in the correlation between progressively low salinities and more rapid death.

There are several indications that the effects of low salinity reach far beyond direct osmotic unbalance. Bethe ('30) showed that the sea slug, *Aplysia,* initially takes up water and then loses, when under hypotonic conditions. This is probably generally true and is in accord with the observations on Thais. It seems apparent that changes in permeability are involved. Scordia ('27) described the effect of low salinity as anaesthetic and akinetic. In an as yet unpublished investigation Hopkins has found that the loss of salts from oysters subjected to low salinity is highly specific and differential. He has also shown ('36) that pumping stops when the salt concentration of the medium drops to about 10 or 13 p.p. 1000. Finally, according to Ishida ('35) oxygen consumption falls off.

From these several results a prediction may be warranted that differential salt loss in diluted sea water may be such as to bring about a relatively high magnesium concentration in the tissues, with consequent well known anaesthetic effects. It will be of interest to note whether this possibility will be borne out by experimentation.

SUMMARY

1. The first effect of low salinity upon the snail, *Thais floridana*, is immobilization. At salinities of 10 p.p. 1000 and below a significant percentage of the snails cannot right themselves nor move about; at 0 and $3\frac{1}{2}$ animals close more or less completely. At 7 and 10 p.p. 1000 they lie open.

2. After several days exposure to salinities which eventually result in death the snails lose sensitivity to mechanical stimulation.

3. With an exposure of 1 to 2 weeks at an average temperature of approximately 20° C., practically all snails at 7 p.p. 1000 and below are killed. With exposures of less than a week, salinities of 0 and $3\frac{1}{2}$ were found to be considerably less lethal than 7. Presumably by inducing maintained closure of the operculum, extremely low salinities bring about a protective reaction against lethal effects.

4. Size is an important modifying factor in resistance to low salinity. Small snails are much more susceptible than large.

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OBSERVATIONS ON THE LIFE CYCLE OF THE FAIRY SHRIMP *EUBRANCHIPUS VERNALIS*

It is well known that in north temperate latitudes the fairy shrimp, *Eubranchipus vernalis*, is an inhabitant principally of small ponds that tend to dry up during summer, and that the adult appears active chiefly in spring after the ice is melted.

In spite of innumerable references to the adults, little has been done on life history. Hay ('89) described most of what is known.

In general, throughout this zone the adults are active in April, breed and produce eggs that have a long dormant period during the summer. And it appears that larval development begins in late fall or early winter, may be retarded under ice and then completed in early spring. See Ferguson, 1939.

The chief ideas regarding special environmental factors necessary for completion of the cycle, are that there be a drying of the eggs and also freezing. Whether one or the other is necessary, or merely a long resting period, is problematical. For example, Hay ('89) found eggs hatching after drying in mud and resting six months. Maybe the resting period alone was the factor needed, and possibly drying was not necessary.

Castle ('38) reported that drying was not necessary to hatch eggs. Avery ('39) reported that the egg developed after one year resting in water without drying or freezing. His material was from ponds that had not dried up for seven years, and, of course, he kept it at temperatures to prevent freezing.

Outline of Work and Observations.—A preliminary study of the ecology of the fairy shrimp was made in the spring of 1940, but all aspects were not completely studied and most of the details secured about the biota of the pond must be omitted here.

The pond, north of Akron, 250 yards east of the Akron-Peninsula Road, in a depression on a ridge, 50 by 35 yards in size when well filled, is supplied with the usual vegetation including some cat tails, and typical submerged plants. It dries out every summer.

Some ice was still present when adult fairy shrimps were seen March 18. Egg sacs were present on females. There were five females to one male. Later more and larger sized adults were seen, and males increased in number, but by March 30 there was some decrease. There was intermingling of the sexes at any depth.

A study of egg hatching under laboratory conditions was conducted (as reported below under Laboratory Experiments on Hatching) when time permitted during the summer of 1940.

Finally, during the fall and winter of 1941 and 1942 observations were made in the field and collections made were studied in the laboratory (as summarized below under Observations on Life Cycle).

Laboratory Experiments on Hatching.—Males and females were swimming about in laboratory jars for a long time in spring. Later eggs were obtained by careful check of all bottom sediment and separation by pipette. About equal numbers of eggs were placed in small jars. Mud used in jars had been previously boiled and thus made reasonably sterile. Tap water was used. To simulate drying out of a pond, evaporation of shallow water from an uncovered jar sufficed. For freezing slowly, jars were put in a deep dish of ice and salt. For rapid freezing "dry ice" was used packed around the jar. Slow or rapid thawing were easily arranged by use of ice box or without.

Slow Freezing and Slow Thawing.—Eggs in a jar were covered with an inch of water. Slow freezing with ice and salt was done on July 30. Conditions were arranged in an ice box for slow thawing. Twelve days (Aug. 12) after treatment a few nauplii appeared. Many eggs remained unhatched. Treatment was repeated August 26. Again twelve days after treatment, September 7, nauplii appeared. Altogether 30 per cent, 10 out of 30, of the eggs hatched.

Rapid Freezing and Rapid Thawing.—On August 26, eggs in a jar were covered with an inch of water. Rapid freezing was brought about in 10 minutes. Later the ice was quickly thawed. In twelve days, on September 7, there was hatching of nauplii, but only from 2 out of 28 eggs, or 7 per cent hatched. One nauplius was seen emerging from its egg.

Drying Out: Water Added.—Eggs were placed in a jar of mud and shallow water July 3. Water evaporated. After about a 20-day period, considerable water was added July 30. In 13 days, August 12, nauplii appeared. The jar was kept. But part of this mud (not water covered July 30) was kept and water was added August 26; thus about 46 days of dry condition occurred. Again after 12 days in water some nauplii appeared, September 7.

Hay ('89) used the same method, but the work was done during the normal time of development of the fairy shrimp. In the present experiment, nauplii appeared in water after drying, during summer an off period for development. Here the resting periods were short, not 6 months or a year.

Drying Out; Water Period; Frozen.—On July

1, eggs in a jar with shallow water were allowed to dry out as in the preceding case. Water was added July 30 and this was frozen, and later thawed. In 13 days, August 12, some nauplii appeared.

The experiment was repeated on another jar of eggs but with more rapid freezing and subsequent rapid thawing. There was distinctly reduced percentage of hatching.

Water; No Drying or Freezing.—Eggs which were placed in plain water after collecting from aquaria where females had shed them, were kept over a long period. They were not subjected to drying or freezing. During the nine months period of observations, no hatching occurred. Circumstances prevented continuing the experiment.

The above experiments yield data only on hatching of eggs, not on survival or development of larvae.

Observations on Life Cycle.—Starting in October 1941, and at intervals until April 6, 1942, collections were made in the pond in the attempt to get life history data from Nature, rather than to depend upon working out some few individuals through a life cycle under laboratory conditions. The latter method was not overlooked and a few larvae secured were kept in small aquaria jars to get acquainted with the succession of larval stages or instars. A complete set of drawings of all stages was planned, but time did not suffice for doing the entire set and adequately checking them.

In the collections all material was carefully collected from the bottom as well as plankton samples taken from the open water of the same areas.

Various stages, referred to here as forms, were taken as follows:

Nov. 14	1 mm. forms
Nov. 23	some 1 mm. and some 4 mm. forms
Nov. 31	7 to 9 mm. forms
Dec. 7	7 to 9 mm. forms
Jan. 31	30 mm. forms, which are adults also 7 to 9 mm. forms
Feb. 15	7 to 11 mm. forms
Mar. 10	7 to 15 mm. forms; mostly 11 mm.
Mar. 14	7 to 23 mm. forms; mostly 15 mm.
April 6	20 to 25 mm. forms; adults

Conclusions and Interpretations.—1. The temporary ponds which fill up well in November and December, due to rains and snow, and have an ice cover, and then have open water conditions in spring for a long time, making favorable conditions for larval development, for adults, and for breeding and egg laying, and which may dry out more or less during the summer, offer the most favorable habitat for the fairy shrimp. That has been long recognized. The ponds are not necessarily dry for a half year or longer, but would frequently be dry for a time.

2. Drying of eggs, freezing of eggs, and a long resting period are all conditions occurring in nature.

3. A resting period from late spring to sometime in fall, or about six months, is a normal event in these latitudes. But this period of time is not absolutely necessary. In the present experiments, instances of hatching occurred after much shorter periods (but with drying or freezing) during the summer. Increased duration of egg stage beyond 6 months may occur. In one experiment reported here (but this without drying), eggs remained unhatched 9 months. Avery ('39) reported hatching after one year (but without drying or freezing). Also eggs may remain unhatched still longer. Long rest or long time above 6 months is not itself necessary but neither is it an inhibitor. But experiments here reported show much shorter periods of time will suffice.

4. Drying is an important factor in hatching, probably essential for eggs laid in spring to be hatched in due time next fall. In the present experiments drying was a factor that induced hatching in even very brief periods, in summer an off season for hatching. In the test without drying, eggs remained unhatched longer than the half year normal period. Also another case reported (Avery, '39) of hatching without drying, shows much retarded hatching; the eggs hatching in April, at a time when nauplii would have insufficient time to develop to adults before temperatures became too high.

5. Freezing is likewise a factor occurring almost as regularly as drying. But we have no proof that necessarily all eggs in mud under a pond coated with ice, are actually frozen. But in the experiments here reported freezing was definitely shown as a factor inducing hatching, accomplishing this in even shorter than normal time, in an off season summer. The same report of Avery of eggs not undergoing drying or freezing should be cited again. Nauplii hatched in April, too late for development to adults in favorable temperature.

6. The period of 12 days to initiate hatching after the stimulation or "shock" of drying, or freezing, or both, seems to have some significance in these experiments, and seems more than a coincidence.

7. Not all eggs are equally sensitive to the "shock" of drying or freezing. The resistance of eggs has ecological significance. If after drying, which induced some egg hatching in a short underwater period in fall, many eggs remained unhatched, then, in the event of another drying off which would kill nauplii, many eggs would survive to hatch in later fall or early winter in water that continued. Possibly also, more than one distinct freezing and thawing might occur in one season.

8. Observations in this case in the winter of

1941–42 indicate two periods of hatching, about the middle of November and about the end of January, with the first group becoming adult about late January, and the second about the beginning of April.

C. RICHARD WEAVER [1]

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[1] This paper as presented was written by Walter C. Kraatz, Head, Biology Department, University of Akron, from three student papers, progress reports of Mr. Weaver, whose entrance into the armed forces of the U. S. prevented his writing of this paper.

LITERATURE CITED

Avery, J. L. 1939. Effect of drying on the viability of fairy shrimp eggs. Trans. Amer. Micro. Soc. **58**: 356.

Castle, W. A. 1938. Hatching of the eggs of the fairy shrimp. Science **87**: 531.

Ferguson, M. S. 1939. Observations on the *Eubranchipus vernalis* in Southwestern Ontario and eastern Illinois. Amer. Midland Naturalist **22**: 466.

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BOOK REVIEWS

FERNS AND FERN ALLIES OF LOUISIANA[1]

A marked interest has developed in recent years in the distribution and, to some extent also, in the ecology of the ferns and fern allies of the United States. Ample evidence of this interest is seen in the many publications which have appeared during the last decade. These range from short articles of taxonomic or ecological interest to more extensive local plant lists and state or regional floras. Although these publications are not in general confined to any particular region, it must be admitted that the majority of the state floras have come from the southern states. Besides contributing facts concerning the occurrence and distribution within their respective areas, these state floras have added much to our knowledge of the general distribution of the ferns and fern allies in this country. Furthermore, they have stimulated interest and further study. The most recent of these is the *Ferns and fern allies of Louisiana.*

This publication is a handsome octavo volume of 186 pages, printed on excellent paper and bound in cloth. It is illustrated with good photographs of nearly all species included. An introduction of over 24 pages discusses the ferns in general, previous studies made of the ferns of Louisiana and their distribution in relation to physiography, soil types and the geology of the state. It is concluded that, in general, some ferns show similar peculiarities in their distribution in Louisiana to that of certain of the higher plants. These peculiarities apply mainly to the northern ferns which are either definitely limited in their distribution or widespread, although both types are more or less restricted to terrace soils. An interesting observation is the absence of some species of wide distribution from the Mississippi floodplain. The much debated question whether the tropical ferns, *Ceratopteris deltoidea* Benedict and *Pteris multifida* Poir. ex Lam., are native or introduced is brought up and, although not definitely stated, it is at least implied that on the basis of distribution, they are probably introduced.

The book is provided with diagnostic keys to the families, genera and species. The descriptions are well written with emphasis on the distinctive features which characterize each entity. These are followed by citations of specimens. Of more interest, however, to the ecologist are the notes on habitats and general distribution Sixty-six species and a few varieties are reported to occur in Louisiana. Fourteen of these have not been reported before from this state. In an appendix is a list of ferns which have not so far been found in the state but which, on the basis of their distribution, are to be expected. Included here is also a list of excluded species.

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BIRD PSYCHOLOGY[2]

As a compendium of the facts of bird display this book represents a distinct contribution to ornithological literature. The labor expended in digesting the contents of the naturalistic and experimental reports which comprise the 30-page bibliography must have been tremendous. The accounts of various aspects of bird display are enriched by frequent reference to similar behavior shown by invertebrates, fishes, reptiles, and mammals.

The author is certainly to be commended for his painstaking and exhaustive treatment of the relevant literature; however, the promise implied in the book's subtitle "An introduction to the study of bird psychology" is not fulfilled.

Psychology is a recognized field of science the major areas of which are reasonably well defined. It is too complex a subject to be successfully treated by any sort of an oblique approach. An adequate discussion of the psychology of birds would have to include consideration of many well-known facts concerning learning ability, innate behavior patterns in addition to display reactions, sensory and motor equipment, memory, developmental history, etc. Those sections of the book which are primarily psychological deal with the interpretation of behavior; and in these interpretative passages there is much to criticize.

Mr. Armstrong presents many excellent descriptions of physical structures or behavior patterns and then customarily proceeds to adduce their "use" or "purpose." For example, the Australian frogmouth's peculiar method of erecting its crown feathers, drooping its wings and opening its beak with the consequent exposure of the mouth markings is categorically interpreted as an endeavor to frighten intruders. In several instances the function of a behavior pattern is described in terms which defy scientific definition. A bird's "dance" is described as ". . . a regulative process by which he controls his vitality and maintains his tension at the requisite pitch."

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[1] **Brown, Clair A., and Donovan S. Correll.** 1942. Ferns and fern allies of Louisiana. Baton Rouge: Louisiana State University Press. xii + 186 pp. $3.00.

[2] **Armstrong, E. A.** 1942. Bird display: An introduction to bird psychology. Cambridge: The Univ. Press. N. Y.: The Macmillan Co. $5.50. Pp. 381.

Scorning the "mechanistic" approach to his subject, the author cannot forego the humanizing influence of anthropomorphic interpretation. He suggests, for example, that when birds sing in concert "they derive aesthetic pleasure as well as psychological stimulation from their united efforts." The rhythmic body movements which both members of the bird pair may display during courtship are said to be caused at least in part by the fact that birds derive pleasure from imitating each other. Again, "aërial evolutions, antiphonal singing and the like are indulged in because birds, like ourselves, feel satisfaction in ordered movement and rhythmic sound. Thus are the bonds of biological utilitarianism broken and birds become artists, acting and singing for the joy inherent in doing so." As has been pointed out so often the danger in such descriptions of the behavior of lower animals lies in the fact that this type of interpretation is not subject to proof or disproof by any means available to science, and that with such a convenient and purely subjective explanation readily available the search for genuine causal relationships is less likely to be pursued.

In Mr. Armstrong's book a great deal of the psychological interpretation of the behavior of birds proceeds from analogies with human reactions. For example, "The emotional processes of birds during courtship may be compared with the situation which arises when two people have a heated argument. As passion mounts they 'forget themselves' and eventually come to blows. The words and gestures which constitute the 'display' of the parties to the altercations express their emotions, and each by his display, arouses further increments of emotion in the other, accompanied by the secretion of adrenalin and other physical changes,[3] until the lengthy passion explodes into violent action. A person, picking a quarrel, may 'work up' his own feelings to a certain point, and apparently so can birds." This form of analogy involves the basic assumption that the physical changes which are known to occur in humans during emotional arousal have their parallel in the courting bird. Although such an assumption is subject to experimental test, the evidence at present is wanting. If objective investigation should show that the expected glandular and circulatory activities do not occur during courtship the entire line of reasoning would fall. A second and less warranted implication inherent in the type of analogy under consideration is the subtle and highly questionable identification of the mental processes of two species which are as widely separated on the evolutionary scale as are man and bird.

Other analogies which are even more objectionable may be typified by the following example. "It is not by accident that there is a resemblance between some of these rites [exchange of incubation responsibility] and the Changing of the Guard. Admittedly there are innumerable differences of detail between the military ceremonial in Whitehall and the etiquette of the woodcock in the dusky spinney, but both are the manifestation of the emotion which concentrates itself about what anthropologists call transition rites or *rites de passage*." This sort of analogy is to be regarded with even more suspicion than the type quoted previously because in the first instance we are at least on solid ground insofar as our understanding of the human behavior is concerned. In the second analogy however, there is not yet available a scientific explanation of either the human or the bird behavior. In fact this constitutes an attempt to explain one unknown in the terms of a second.

A third type of comparison which Armstrong employs freely is almost mystical and offers absolutely no aid to our understanding of bird psychology. The following quotation is a good example. "Whatever the type of the dance, long-term or short-term, erotic or bellicose, solo or social, performed by man, ape or bird there is one generalization which we can make. In the dance the individual reaches out beyond his isolation and seeks to realize that harmony between himself and the external world without which neither health nor happiness can be achieved and on which the perpetuation of the race depends."

In attempting to devise an explanation of many types of display the author employs vague concepts which have little or no basis in scientific fact. Recurrent appeals to psychoanalytical literature do not strengthen his case. In the discussion of disablement reactions and injury feigning he suggests that "the theory which can best explain all these facts is that there exists in birds an undifferentiated store of emotional energy or *libido*, seeking to express itself, but sometimes unable to do so adequately, and at other times diverted into inappropriate channels." Everyone who has studied the behavior of lower animals has probably at one time or another observed reactions which give the impression that Armstrong is attempting to express. Nevertheless, in the interest of the advancement of scientific knowledge it is better merely to describe objectively the responses and to eschew premature interpretation. It is especially undesirable to advance purely hypothetical explanations based upon concepts which in themselves are totally unscientific.

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[3] **Cannon, W. B.** 1929. Bodily Changes in Pain, Hunger, Fear and Rage. 2nd Ed. Appleton & Co., New York.

There is one other general element of weakness in Mr. Armstrong's book. He is particularly interested in the evolution of behavior patterns. The importance and fascination of this aspect of the problem are undeniable, but equally apparent is the danger of imaginative speculation as to the probable course of the evolutionary process. It benefits us little, for example, to surmise that nest building has evolved from a tendency to fidget with grass and twigs under conditions of emotional stress; and it is definitely misleading to suggest that "an elaborate system of ceremonial signaling *has been evolved in order that* (ital. mine) the rhythms of the male and female might be synchronized and the perpetuation of the race thus assured." The circularity of argument is obvious and the injection of the purposive element most undesirable.

In summary it may be said that ornithologists can benefit from Mr. Armstrong's careful survey of the literature, but that his attempts to employ the material so assiduously collected in the formulation of psychological theories are in the main unsuccessful.

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MAN AND CLIMATE[1]

No topic of human speech is more common than the weather, it matters not whether men be gathered at a Kalikak Family Reunion or at a dinner party of Boston Brahmans on Beacon Hill. The author of this popular work has devoted a useful life to the study of this subject in widely varied regions of the world and he endeavors to give the layman some of his findings and conjectures. His book is divided into three parts. Part I opens appropriately enough with a kind of hymn to the Sun, following which the author introduces Ivan and Hilda, a pair of Wistar rats who serve the double purpose of providing comic relief and a symbol of Research to the reader. Ivan and Hilda and their numerous cousins, always cheerful in adversity, are subjected to all manner of indignities of laboratory heat and cold, and seem to produce data to support some interesting theories. In a fairly cool environment, these rats were healthy, happy, hungry, fast-growing, lusty and fruitful. When shifted to heat of tropical intensity, they were subdued, they ate less, were less fecund, and produced scrawny offspring, and were less able to throw off disease. With these facts in mind, the author made a study of animals in the tropics, and he found that chicken, hogs and cattle mature more slowly, and that meat and eggs produced in such regions are low in vitamin content. Further study proved that men of the tropics suffer more from want of vitamins, particularly the B vitamins, than men in other latitudes. The author's interest then turns to the question of the age of maturity in the tropics. He finds that illegitimate first births in Cincinnati (which town he considers as belonging to the Temperate Zone, though some who have summered there may disagree) come at an average maternal age of 15, and that the corresponding births in tropical regions come at the age of 19. These and other findings are highly interesting. It is to be regretted that the author has not supplemented his pages on the effect of heat and cold on mice and men with a few clear and simple tables of actual data; that would have added considerably to the reader's understanding. But like some august Moses, descending from a awesome Mount Sinai of Science, he brings the Law and nothing more.

Part II contains for the most part further varied observations made in temperate and torrid zones concerning climate and its effect. Here some parts are rather commonplace and not too interesting: pages are devoted to the revelation that coffee contains caffeine, and that caffeine often brings sleeplessness and may in time injure the heart (Chapter VII); Mr. X, a manufacturer of Cincinnati, who suffers a good deal from sinus infections, is advised to move to the Southwest (Chapter VIII); a sinister combination of winter soot and fog, designated as "smog," is a serious menace to many cities in northern regions (Chapter XI); work-horses, cattle, pigs, chickens and even men may die during a severe heat-wave in a so-called temperate climate (Chapter XII). There is little here that the reader has not long ago taken for granted, just as he has the fact that people commonly wear heavier clothes in winter than in summer. On the other hand, some of the paragraphs in Chapter XIV (Climate and Human Reproduction) in which Doctor Mills restates some of the ideas made familiar by Ellsworth Huntington, may prove fresh and fascinating, and may cause some of the fortunate who read them to bless their foresighted parents if, like 27 out of the 31 Presidents of these United

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[1] **Mills, Clarence A.** 1942. Climate makes the man. Harper and Brothers. 320 pp.

States, they were conceived in the salubrious eight months between December and July. All in all, there is not a great deal in Part II that is not a part of common knowledge, although it may inspire some sound reflection on the myriad ills to which the flesh is heir.

Part III is more readable and in a way more interesting, thanks to the author's imaginative powers and to his ingenious combination of fact and conjecture. He sets out with ten good pages on Sunspots. Then he launches into what may be a strictly personal theory of long-range climatic cycles. Doctor Mills has no use at all for gentle climates, and is convinced that long periods of mild weather affect individuals and nations alike, bringing inertia and decay. He believes that Greece and Rome flourished because the climate there was far cooler and more stimulating in the period of their greatness than it is to-day. The last millennium of abnormal warmth, he states, maintained in Europe from the time of the fall of Rome until the Renaissance, and that is the reason why civilization in that interval slumped into the Dark Ages. On the other hand, protracted periods of exceptionally cool weather may stimulate mankind to sudden feverish activity. For example, in the XVIII Century there were daily thermometer recordings made at Zwannenberg, less than 300 miles from Paris. There, in the 34 years from 1750 to 1783, only eight scattered years showed recordings of mean annual temperatures below normal. In 1784, however, there began a prolonged period of chilly weather which was extremely pronounced in the year 1789. Hence the French Revolution: agitated by climatic stimulation, man had to assert himself. It is interesting to imagine the effect of this theory on the too willing reader: provided his thermometer falls to an unseasonable mark and remains there a while, he may sprint down to the corner of Main and Washington Streets some brisk morning, hoping to be there in time to help the boys throw up the first barricade.

As Part III progresses, Doctor Mills' theory is further applied to Napoleon's Campaign in Russia, to the First World War and to the present conflict. And through these pages runs a warning, as sinister as the tragic notes often repeated in Beethoven's Fifth Symphony. For the author senses a change in the climatic tide of our time that is far from cheering. We are probably swinging away from the invigorating weather that made our immediate forefathers do great and mighty things toward a new long spell of milder winters and hotter summers, perhaps to the new Dark Ages. Already, he feels, man is falling away from the mental and physical heights he has lately attained: an extensive survey which Doctor Mills has made shows that in the State Universities of North Carolina, Kentucky and Kansas, the height of freshmen girls became stable about ten years ago, and that male freshmen in these same schools reached a fixed point in height about eight years back; regression appears now to have begun. Thermometer and yardstick seem indeed to demonstrate that civilization has again passed one of its several noons and is gradually verging toward another lovely sunset. In short, as Doctor Mills' most lowly reader will readily see, the heat is on, and in due season our goose will be cooked to a turn. Such dreadful news will be all the more shocking to those who have found such comfort lately in those advertisements that have scattered so much cheer in depicting the brave new world of plastics and pretty platitudes that was to have emerged in the good time after the War.

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Migrations of Lepidoptera[1]

The extensive journeys or mass movements which are performed by many species of animals have always presented many aspects of interest to ecologists. The migrations of birds, fishes, and insects are frequently of economic importance, the means by which the individual animal is oriented during such migrations is often a physiological puzzle, and the origin of an instinct which sometimes appears to be unnecessary or to lead to biological waste has long been a subject of speculation.

Since actual data on the migrations of animals other than birds are all too scarce the present publication should receive a warm welcome. As one reads through this paper, which is largely supplementary to C. B. Williams' 1930 monograph on butterfly migration, one cannot fail to be impressed by the increased rate at which data on the subject are accumulating. A bibliography containing an estimated 600 references is entirely supplementary to the bibliography in the earlier monograph and numerous references to coöperation received from persons and institutions indicate a rapidly growing interest in the field. Still, the study of migrating Lepidoptera is in its very early stages. The descriptive side of the picture is still emerging and the analytical study of the phenomena is just getting under way.

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[1] **Williams, C. B., Cockbill, G. F., Gibbs, M. E., and Downes, J. A.** 1942. Studies in the migration of Lepidoptera. Trans. Roy. Ent. Soc. London 92 (1): 101–283.

In 1931 when Heape drew the distinction between emigration and migration only one lepidopteran was listed as a true migrant. Although he rejects Heape's terminology, Williams now provides evidence that many lepidoptera do actually migrate in any sense of the word. The evidence for a return flight seems good for 10 species where records are adequate and there are suggestions that other species also perform a round trip. One cannot entirely agree with Williams' evident feeling that return flights must occur because if the individuals flew away to die the migratory habit would be nonadaptive. He states (p. 250): "Modern theories of evolution, from Darwin to the statistical geneticists, demand a survival value for any characteristic which is to persist." Actually nonadaptive characters do occur, usually no doubt, as incidental results of gene combinations which are adaptive in other respects. It may also be noted, however, that a character will usually not disappear immediately after it has ceased to have survival value. If, as has often been suggested, migratory tendencies may be characters of this sort it seems rather idle to speculate on how many years should elapse before the instinct is lost in any particular case.

The present picture of lepidopteran migration shows many species migrating in great numbers in certain years. The flights may be over 1000 miles in length and the direction is largely independent of wind direction and topography. A return flight may occur at a different season and is usually less conspicuous than the original emigration. The sunspot cycle does not control the years of great movements and the stimulating factors apparently differ for different species as the migration years may not coincide even in the same region. However, there is evidence for some widespread influential factor because there is a significant positive correlation between flights in the U. S. and in Europe. Possible relationships of these migrations to breeding or to alimentation are rather obscure.

Some work has been started on the experimental analysis of these migration problems and preliminary results are presented and discussed. Experiments on young locusts have failed to show response to magnetic fields as a possible means of orientation. An apparently satisfactory method of marking butterflies has been developed but has not yet been used on a large enough scale to yield important results. A suggested classification of flight density is based on the number of individuals crossing a line of known length per unit time. The statement that data so collected are independent of wind velocity may surprise the reader. The statement, of course, applies only to local winds which do not affect the entire flight of butterflies. In order to compare densities at different times or in different regions it may be necessary to make corrections for the factor of wind.

The authors present their complete data in some detail and show a thorough appreciation of sources of error. The paper is thus a rich source of information and an important landmark in the study of insect migrations. It contains numerous observations on natural history, distribution, and speciation which add interest for the reader.

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COMPARATIVE ANATOMY OF VERTEBRATE PHOTORECEPTORS[1]

This handy little monograph would perhaps more fittingly be named, "The comparative anatomy of vertebrate photoreceptors," for the names of such conspicuous recent contributors to retinal physiology as Adrian, Bartley, Granit, and Hartline are absent from the bibliography and no mention of electrical studies appears in the text. In fact only 19 of the nearly 250 references given are to articles published in the present decade. Within the intended scope of the volume, however, the relevant literature is well surveyed. Much of the older work, partly forgotten, has been extracted and the facts marshalled in detail, especially on the quantitative anatomical relations of the visual cells and their retinal connections. The book will be a valuable source of such information to all who deal with vision experimentally.

A chapter relating retinal structure to behavior in various animal types is provocative and one wishes the author had been able to push the discussion further. In the following chapter on, "Photomechanical responses in the retina," the case for a nervous control of pigment migration and receptor cell movements is clearly presented. The relation of hormones and neurohumors to pigment behavior is not considered.

Chapters 8 and 9, on visual acuity and the significance of the fovea, help to relate the anatomical details with the physiological performance of the retina. The author favors Walls' theory, that the fovea serves to increase the resolving power of the retina by refracting incident rays, rather than that it serves to eliminate non-receptor structures in the retina from the light path. Elliott-Smith's view, that the appearance of the macula entailed marked evolutionary advance in the anthropoid brain, is examined critically and rejected.

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[1] **Detweiler, Samuel R.** 1943. Vertebrate photoreceptors. New York: The Macmillan Co. x + 184 pps. 110 figs. $4.00.

The final two chapters, before a recapitulation, are concerned with the retinal pigments, their nature, comparative distribution, cyclic changes in vision and, particularly, the relation of vitamine A to photochemical changes and the defects which result from its deficiency. Work from the author's laboratory strongly indicates that the droplets seen by Kolmer on and between rods are retinine, the carotinoid discovered by Wald, which is formed from visual purple by light and which forms vitamine A in the dark.

The volume is well printed with clear type and is richly illustrated, especially with numerous photomicrographs of the retina, largely from the author's own collection. Perhaps these account for the relatively high price.

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SYNOPSES OF NORTH AMERICAN BIOTIC PROVINCES[1]

In a small volume Professor Dice has outlined twenty-nine "biotic provinces" of the North American continent. At some time or another he has personally visited nearly all of them for observations and has conducted extensive research in many of them. The author is well known for his studies in biogeography, especially of mammal populations, and he has previously published on the characteristics of several biotic provinces. The present work brings up-to-date and revises the biotic areas of North America according to a geographic and environmental point of view. A folding map clearly marks out the boundaries of the twenty-nine provinces as now conceived by the author. The text consists of a series of descriptions of the various provinces.

Many students of biogeography will undoubtedly question some of the boundary lines, while others will question the practice of grouping natural areas by geographical regions rather than by biotic communities. Some of the provinces are relatively uniform in environmental and biotic conditions and would probably remain as a unit under other criteria of classification. Others, however, are arbitrarily bounded and include such a wide range of topographic, climatic, and biotic conditions with a resulting variety of climaxes that grouping them together into a single province would seem to have little value other than a convenient means of location. The author is frank to admit that his groupings are "experimental" and open to revision. The biome concept adopted by many ecologists is not recognized although comparisons are made with studies based upon that concept. The provinces in some cases include several unrelated biotic climaxes because of proximity and exclude related climaxes which are geographically removed. This is the first book which attempts to divide the biota of the entire continent on the basis of regions, which is more akin to the method of the geographers rather than that of the biologists.

The synopses are brief and non-technical. They are descriptive and general in nature, uniform and well balanced, throughout. The derivations and in some instances the synonomy of the names of the provinces are explained. Subdivision of the provinces has been made according to available knowledge on each region. Where little research has been done, no attempt is made to organize subdivisions. Many references to original literature, especially the older literature, are given, but it seems to the reviewer that too few sources have been utilized in as much as the textual material is chiefly a guide to published works of a biogeographical nature. The Naturalist's guide to the Americas can well be used as a companion volume although it is not suggested as such, and only two references are given from this compendium. Comparisons are frequently made between certain provinces as described and other systems of classification or other interpretations, but with few exceptions they are not compared in their entirety.

Consideration is given to predominant vegetation, characteristic mammals, and birds with emphasis upon the first two, which are the only ones to be given specific mention. The bulk of the literature cited is also concerned with those three groups. Typical pictures of at least some of the provinces would have been worth the increase in cost of the volume. Physiographic and climatic maps, and perhaps a soil map as well, on the same projection and scale as the one of the provinces would have made interesting comparison had they been included. According to the author they formed much of the basis for his map of biotic provinces. There is a good subject index.

This study makes two significant contributions. First is the map which summarizes many years of extensive field work by the author and his students, setting forth his conclusions regarding the grouping of natural areas. Second, and most important, it is a stimulating essay which will undoubtedly arouse much interest in biogeographical studies and furnish abundant food for thought for ecologists including those who prefer a community rather than a regional point of view.

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[1] **Dice, Lee R.** 1943. The biotic provinces of North America. Ann Arbor: Univ. of Michigan Press. viii + 78 pp. 1 fig. $1.75.

BOOK NOTICES

Errington, Paul L. 1943. An analysis of mink predation upon muskrats in North-Central United States. Iowa Agricultural Experiment Station Research Bulletin No. 320. Pp. 127. (Copies can be obtained free-of-charge as long as the supply lasts upon individual request to the "Bulletin Office, Iowa State College, Ames, Iowa.") Ecologists will welcome this cogent analysis by Professor Errington of predation pressure in vertebrate populations. The bulletin is excellently documented and collates much that would be otherwise inaccessible. The author shows a commendatory interest in interpretation as well as in fact. Among his conclusions, these may be summarized as especially interesting. (1) ". . . strangeness of environment, intraspecific intolerance, and drought were especially important in predisposing muskrats . . . to predation." (2) ". . . kinds and numbers of wild predators . . . had little bearing upon the net mortality suffered by the muskrats." (3) ". . . severity of predation may leave highly misleading impressions as to population effect" [due to such factors as "intercompensatory" or automatically adjusting trends]. "Even when locally nearly annihilative, predation rarely showed evidence of functioning as a true population depressant." (4) "On the whole, any factor, whether of 'natural' origin or associated with man, that promoted instability in muskrat populations heightened vulnerability to predators, and the resulting losses were likely to show a high degree of intercompensation." A stimulating study!—T. P.

Walker, Helen M. 1943. Elementary statistical methods. N. Y.: Henry Holt & Co. Pp. xxv + 368. $2.75. In keeping with its policy of noticing new books on statistical method, ECOLOGY calls its readers' attention to the volume by Walker. The standards set for the book are: (1) complete clarity for the beginner and such simplicity of exposition as will make the text practically self-teaching, (2) more than ordinary attention to the development of underlying concepts and to interpretation, (3) such harmony with recent developments in the mathematical theory of statistics as will insure a satisfactory foundation for more advanced study, (4) the presentation of a fundamental core of introductory material which can be covered by an average class in one semester, and (5) the inclusion of other material to serve as reference and as invitation to further study. The book lives up in general to these desiderata. It emerges as a clear discussion of large-sample methods. There is no detailed treatment of small-samples, chi-square or the analysis of variance—methods of proved value for the ecological investigator. Most of the illustrative data are from the area of educational statistics. The diagrams and tables are well done. There is an appendix of statistical tables, a glossary of symbols and an adequate index.—T. P.

Smith, Roger C. 1942. Guide to the literature of the zoological sciences. Minneapolis: Burgess Publishing Company. Pp. vii + 128 (mimeotyped). $2.00 (paper). This is a manual to be placed in the hands of the zoölogist, whether student, teacher or investigator, to assist him to deal efficiently and comprehensively with his particular bibliographic problem. We recommend particularly that the beginning graduate student familiarize himself with the book's contents. It should serve him well as his career progresses. (We are, of course, additionally impressed by the volume since it states that ECOLOGY is ". . . the leading ecological periodical in the United States.")

Pearse, A. S. 1942. Introduction to parasitology. Springfield, Ill.: Charles C. Thomas. Pp. ix + 357. This book is particularly noteworthy in that it is comparative in its treatment of parasitology. One finds non-human parasites discussed whenever they illustrate a particular point of interest. Also, a good discussion of human infesting forms is included. The story is developed on a systematic basis starting with Protozoa and ending with Chordata. The various discussions are not exhaustive and are intended as introductions primarily. The book serves as a place for ". . . looking up things, whether it is used in a class-room, on a farm or a fishing boat, in a packing house or a seaside laboratory."

Dublin, Louis I. 1943. A family of thirty million. N. Y.: Metropolitan Life Insurance Company. Pp. xvi + 496. An extensive account of the activities and history of the Metropolitan Life Insurance Company prepared in celebration of its seventy-fifth anniversary. Part V with chapters on "A program of welfare," "Progress in health and longevity" and "The people we insure" contains some information of interest to the biologist.

Tehon, Leo R. 1942. Fieldbook of native Illinois shrubs. Urbana, Illinois: Illinois Natural History Survey Division, Manual 3. Pp. vi + 307. 6 colored plates, 72 figs., map. This simply and clearly written pocket manual may be used by any intelligent amateur naturalist, but is of such scientific accuracy and soundness that it will be very useful to professional botanists. Although the author does not define his concept of shrub, he makes some mention of 210 species and 27 varieties of native and definitely naturalized shrubs, a seemingly large number in a prairie state. The number is not surprising, however, when one remembers that Illinois possesses a great diversity in habitats, although many are limited in extent, such as the bogs in the northeastern part of the state. Most of the species are illustrated by neat line drawings of leaves or twigs in the summer condition, or of other diagnostic features. Descriptions are written in complete sentences to appeal to the layman, and non-technical words are used when possible to do so without loss of accuracy. A glossary of necessary technical terms is appended. The book should be useful in neighboring states as well as in Illinois.—C. E. O.

Webster's Dictionary of Synonyms. 1942. Springfield, Mass.: G. & C. Merriam Co. Pp. xxxiv + 907. This is a very helpful reference for all who write. It enables one to pick the precisely suitable word by means of the clear comparisons which are made between words of a common denotation, thus enabling one to distinguish differences in implication, connotation, and application. There are also lists of analogous words, antonyms, and contrasted words.

Clarke, S. E., E. W. Tisdale, and N. A. Skoglund. 1943. The effects of climate and grazing practices on short-grass prairie vegetation in southern Alberta and southwestern Saskatchewan. Dominion Department of Agriculture. Technical Bulletin 46. 53 pp., illus. **Young, V. A., G. B. Doll, G. A. Harris, and J. P. Blaisdell.** 1942. The influence of sheep grazing on coniferous reproduction and forage on cut-over western white pine areas in northern Idaho. University of Idaho Bulletin XXXVII (6), Forest, Range and Wildlife Experiment Station Series No. 1. 46 pp., illus. **Martin, W. P., and Joel E. Fletcher.** 1943. Vertical zonation of great soil groups on Mt. Graham, Arizona, as correlated with climate, vegetation, and profile characteristics. University of Arizona, Agricultural Experiment Station, Technical Bulletin No. 99. Pp. 89–153, illus. Although these bulletins all are concerned with intensive investigations on relatively small areas, they contain data of fundamental value and interest to students of vegetation, soils, and forest and range management. They deserve a wide distribution.

In the July 1943 issue of ECOLOGY there were two book notices of publications by William M. Rush: "Wildlife of Idaho" and "Wild animals of the Rockies, adventures of forest ranger." These notices were kindly prepared by Doctor H. L. Shantz whose initials were inadvertently omitted at the end of the review. The error is regretted.

EDITOR

PROCEEDINGS, PART II

Ecological Society of America, 1942

Report of the Treasurer

Ecological Society of America
Royal E. Shanks, Treasurer

Statement of Cash Receipts and Disbursements

For the period December 1, 1941 to November 30, 1942

Balance, November 30, 1941		$1,925.44
RECEIPTS		
Dues	$2,986.20	
Income—Florence Building Trust	16.00	
Royalty—*Naturalists' Guide*	32.25	
Interest on Savings Account	15.30	
Rebate on mailing permit	4.33	
Total Receipts		$3,054.08
Total Cash		4,979.52
DISBURSEMENTS		
Ecology	$1,521.00	
Ecological Monographs	474.00	
Bulletin and Secretary's Office	689.70	
Treasurer's Office	154.41	
Committee for the Study of Plant and Animal Communities	94.57	
Committee for Western Section	47.75	
Committee on the Preservation of Natural Conditions	49.95	
Committee on Nomenclature	19.00	
Nominating Committee	1.20	
Naturalists' Guide, purchase and other expenses	207.71	
Contribution to *Biological Abstracts*	100.00	
Total Disbursements		$3,359.29
Balance, November 30, 1942 (less outstanding checks which cleared later)		$1,620.23
Represented By:		
Checking Account, First National Bank, Clarksville, Tennessee (less outstanding checks)	$ 588.20	
Savings Account, Park National Bank, Knoxville, Tennessee	1,032.03	
Total Cash in Bank, November 30, 1942		$1,620.23

August 20, 1943

Mr. Stanley Cain, Treasurer
Ecological Society of America
Knoxville, Tennessee

Dear Mr. Cain:

I have examined the books and records of the Ecological Society of America for the fiscal year ended November 30, 1942.

The statements submitted by Mr. Royal E. Shanks for this period are in agreement with the records of cash receipts and disbursements on the bank statements. Both opening and closing balances of the bank accounts are supported by bank statements, and the closing balances are certified to in a letter dated December 16, from Park National Bank of Knoxville.

Harvey G. Meyer
Certified Public Accountant

REPORT ON THE NATURALIST'S GUIDE

When Williams and Wilkins Company, publishers of the *Naturalist's Guide*, announced their intention to destroy the remaining sheets of the book unless the Ecological Society wished to obtain possession of them, the Executive Committee of the Society took action and at a nominal cost for binding and shipping secured 126 leather-bound and 520 paper-bound copies, or a total of 646.

These books are now stored at the Vivarium Building, Wright and Healey Streets, Champaign, Illinois, under charge of Dr. S. Charles Kendeigh, Chairman, Committee for the Study of Plant and Animal Communities. The Executive Committee agreed to stand the expense of materials necessary to arrange the storage space while the University of Illinois supplied the labor. The books have now all been placed in wrappings with address labels on the outside ready for mailing and are under essentially fireproof and water-proof protection.

The expenses involved by the Ecological Society in securing these books and arranging for this storage are as follows:

Williams and Wilkins Co., for binding	$140.00
Shipping charges (Baltimore to Champaign)	31.54
Lumber and hardware	8.36
Graham Paper Co., for book wraps	27.75
Champaign Letter Shop, for address labels	6.75
Sealing tape for book wraps	1.68
	$216.08

In addition, three leather-bound and one paper-bound copies were given to four graduate and advanced students in payment for several hours' work in cartage of the books and putting them in their mailing wraps. Five books were sold between September and December so there are now 637 copies on hand.

The Chairman agreed to handle the remaining copies of this book with the understanding that proceeds from their sale over the cost of the books and expenses incurred for wrapping and mailing will be credited to the account of the Committee for the Study of Plant and Animal Communities and to the account of the Committee on the Preservation of Natural Conditions over and above their regular budgets annually appropriated by the Society. The sharing of this income will be arranged by the chairmen of these committees on the basis of their respective needs or by equal division.

The Executive Committee of the Society has set a price of $2.50 for the leather-bound copies and $1.50 for the paper-bound copies. Mailing charges may be carried by the Society when payment accompanies the order for a book, but otherwise they may be collected by the Treasurer when he bills the purchaser. All moneys will be turned over to or collected by the Treasurer of the Society and orders may come to him directly.

Furthermore, the understanding with the Chairman was that complimentary copies may be sent out under the jurisdiction of the Committee for the Study of Plant and Animal Communities and the Committee on the Preservation of Natural Conditions, subject to the approval of the Executive Committee, to individuals and organizations associated with the work of the committees or to whom it would be advantageous to do so. As near as estimates can now be made as to the number of books that may thus be required, they are as follows:

Committee for the Study of Plant and Animal Communities	40
Committee on the Preservation of Natural Conditions for the United States	200
Committee on the Preservation of Natural Conditions for Canada and Newfoundland	10
Total	250

A request has come from Mr. William Vogt, Associate Director, Division of Science and Education, in the office of the Coordinator of Inter-American Affairs, for fifty copies for free distribution to universities, geographical societies, and influential individuals south of the Rio Grande. Since ecology is relatively little known in these countries and in view of the recent convention of American republics held in Washington wherein a strong movement was started for the preservation of natural areas in these countries, the chairman recommends that this request be granted.

Shipping funds will be provided for books sent out from the office of the Coordinator of Inter-American Affairs. For the 250 copies to be sent out by the committees above mentioned, the mailing cost will be approximately $30.00. The Chairman requests that this expense be borne by the Society by funds outside of those regularly appropriated for the work of the Committees.

It seems unnecessary to present further arguments for this use of the books. Printed in 1926, much of the descriptive material dealing with natural areas will become out of date when the inventory the present chairman is working on is completed. Descriptions of the various regions, however, will be as valuable in the future as in the past, while the statements of principles and policies are important in influencing the layman, politician, and scientists in the work of the committees and the Ecological Society. Since the Committees have no funds for acquiring and preserving areas directly, they can accomplish these ends only through other organizations and individuals and by the education of others to their viewpoints.

We request, therefore, that this program be approved.

Respectfully submitted,
S. CHARLES KENDEIGH, *Chairman,*
Committee for the Study of Plant and Animal Communities

The Report on the *Naturalist's Guide* was approved by the Executive Committee on February 25, 1943. Dr. Kendeigh is to be commended for the efficient handling of the details set forth in the report and is entitled to the gratitude of the Society for the responsibility he has assumed in taking charge of the books.

The Secretary wishes to remind members that copies of the *Naturalist's Guide* may be purchased either from Dr. Kendeigh or from the Treasurer, Dr. Stanley A. Cain, University of Tennessee, Knoxville, Tennessee. Leather-bound copies are $2.50; paper-bound are $1.50. Postage will be prepaid if the remittance is sent with the order.

RESOLUTIONS

The following resolutions presented by the Committee on the Preservation of Natural Conditions for the United States were approved by the Executive Committee on February 25, 1943.

WILLIAM A. DREYER, *Secretary*

I

Whereas the Ecological Society of America believes that National parks and monuments serve a higher public good if preserved in an unimpaired condition rather than subjected to commercial exploitation, and

Whereas the reports of the study committee of this Society recognize the need for and favors an attempt toward adding a part at least of the Tularosa Malpais to the White Sands National Monument,

Therefore, be it resolved by the Ecological Society of America, that the Society, through the Committee on the Preservation of Natural Conditions, take all needed and desirable steps to encourage the addition of a part of the Tularosa Malpais to the White Sands National Monument, and, that the Society formally recommend that the Tularosa Malpais be placed within the National Park Service.

II

Whereas the Ecological Society of America aims to encourage the preservation of natural areas of biological, scenic and historical value, and

Whereas the South Calaveras Sequoia Grove of California is unique in its possession of the last large tract of sugar and yellow pines in their finest development, representing perhaps one of the oldest primitive forests in the United States, and

Whereas the South Calaveras Sequoia Grove is in immediate danger of being cut over,

Therefore, be it resolved by the Ecological Society of America, that the Society go on record as favoring action by Congress and by other bodies in support of the formulation of necessary arrangements for including the South Calaveras Sequoia Grove within the nearby Big Trees State Park, and handled as an inviolate wilderness area.

III

Whereas the Ecological Society of America believes that National Parks and Monuments serve a high public good, and

Whereas there is an important need for the preservation of seashore areas in their natural condition, and

Whereas the proposed National Seashore Park of New Jersey, Maryland and Virginia represents an area worthy of high consideration from a standpoint of biological and scenic values,

Therefore, be it resolved by the Ecological Society of America, that the Society go on record as favoring Congressional and State Action directed toward the establishment of the National Seashore Park.

IV

Whereas the Ecological Society of America aims to encourage the preservation of representative natural areas when their type is in danger of destruction, and

Whereas legislation is pending for the purchase of the Kitchen Creek Virgin Forest area by the State of Pennsylvania to assure its preservation, and

Whereas the Kitchen Creek Virgin Forest area contains about 1,200 acres of fine virgin hemlock—hardwood forest typical of that formerly prevailing in Pennsylvania, being one of the most scenic areas of its kind in the Northeastern United States, having original flora and fauna typical of northeastern Pennsylvania,

Therefore, be it resolved by the Ecological Society of America, that the Society, through the Committee on the Preservation of Natural Conditions, take all possible and desirable steps to encourage the purchase of this Forest by the State of Pennsylvania to permit it being set aside as a State Forest Park.

V

Whereas the Ecological Society of America aims to encourage the preservation of representative natural areas when their type is in danger of destruction, and

Whereas there is need for encouraging legislation aiming to purchase Silver Lake Virgin Forest as a State Reserve, and

Whereas Silver Lake Virgin Forest comprises about 800 acres of virgin hemlock and hardwood of unusual scenic and biological value,

Therefore, be it resolved by the Ecological Society of America, that the Society, through the Committee on the Preservation of Natural Conditions, take all possible and desirable steps to encourage the purchase of this forest by the State of Pennsylvania to permit it being set aside as a State Forest Park.

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